University of Alberta

Ecology of *Parelaphostrongylus tenuis* (Nematoda: Protostrongylidae) in white-tailed deer and terrestrial gastropods of northern Michigan with implications for moose

By

Pamela Jane Boppel ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Ecology of *Parelaphostrongylus tenuis* (Nematoda: Protostrongylidae) in white-tailed deer and terrestrial gastropods of northern Michigan with implications for moose** by Pamela J. Boppel in partial fulfillment of the requirements for the degree of Master of Science, Environmental Biology and Ecology.

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Abstract

Moose were reintroduced to Michigan's upper peninsula in 1985 and 1987. Meningeal worm, *Parelaphostrongylus tenuis*, is a major cause of mortality for this moose population. The ecology of *P. tenuis* was studied in 1995 - 1996, in the definitive host, white-tailed deer (*Odocoileus virginianus*), and in gastropod intermediate hosts to determine whether seasonal distribution of white-tailed deer, or distribution of infected gastropods could result in increased exposure of moose to this parasite.

Sixty-nine of 158 (44%) deer were found to be infected with adult worms. Average intensity was 1.7 (± 1.1) worms per deer. Prevalence did not differ by gender of deer or geographic location within Michigan's upper peninsula. Prevalence was lower in fawns than yearlings or adults and all fawns had single worm infections. Numbers of larvae in feces of deer increased February through May when deer normally disperse from wintering areas; this ensures that gastropods are exposed to the parasite over wide areas.

A total of 9,552 gastropods were collected from three broad habitat types and in areas where deer congregated or areas inhabited by moose. Greater numbers were collected in lowland areas of various habitat types. Overall, less than 1% were infected; most had 3 larvae or fewer. Lowland areas where deer congregated during winter (deer "yards") tended to have higher numbers of infected gastropods than other areas, but their role in transmission of *P. tenuis* to moose is probably limited because deer yards are spatially separated from primary moose range. Infected gastropods were found in areas inhabited by moose therefore, moose are vulnerable to infection within their preferred range. Random, low-level exposure to *P. tenuis* is probably the most common route of transmission for moose to acquire infection.

Greatest numbers of infective larvae were found in gastropods during August which indicates highest potential transmission to definitive hosts, especially fawns and calves, is in late summer and early autumn.

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CHAPTER I. GENERAL INTRODUCTION

Meningeal worm, *Parelaphostrongylus tenuis* (Nematoda: Protostrongylidae) is a unique and well-known parasite that inhabits the central nervous system of wild ungulates. It is well-documented that this nematode causes few problems for its natural host, the white-tailed deer (*Odocoileus virginianus*) (WTD) (Anderson 1963a), but often causes fatal neurologic disease in many other ungulate hosts, including moose (*Alces alces*) (Anderson 1965, 1972). The ecology of this parasite is receiving more attention in the literature as researchers attempt to unravel complex aspects of transmission. In general, deer and other hosts such as moose acquire *P. tenuis* by accidentally ingesting terrestrial gastropods that serve as intermediate hosts (Anderson 1963a).

The logistics and timing of transmission between intermediate and definitive hosts remain speculative. Often over 50% of WTD in a population are infected with *P. tenuis* (Anderson and Prestwood 1981) and large numbers of larvae are found in feces of WTD (Peterson *et al.* 1996). In contrast, few infected gastropods are found in nature, particularly in certain areas (Gleich *et al.* 1977, Kearney and Gilbert 1978, Pitt and Jordan 1994). This raises the question of when and where sympatric moose are most likely exposed to gastropods infected with *P. tenuis*.

Sympatric populations of deer and moose have persisted in numerous places throughout northeastern North America (Anderson 1965, Karns 1967, Gilbert 1974, Upshall *et al.* 1987, Thomas and Dodds 1988), however, many agree that *P. tenuis* probably limits the growth of moose populations (Anderson 1972, Whitlaw and Lankester 1994). Risks for moose acquiring *P. tenuis* can only be evaluated following closer examination of spatial distributions between infected WTD, gastropods and moose.

Life Cycle and Pathology of *Parelaphostrongylus tenuis*

Parelaphostrongylus tenuis is a parasitic nematode of ungulate definitive hosts, the natural host being WTD. Adult worms inhabit the cranial cavity associated with venous blood sinuses and connective tissue (*i.e.*, meninges) (Anderson 1963a). Females deposit eggs into veins and eggs are carried to the lungs where they develop into spine-tailed first-stage larvae (L1s) within the alveoli (Anderson 1963b). Larvae are moved out of the lungs by the ciliated lining of the "bronchial escalator" (Anderson and Lankester 1974), are coughed up, swallowed, and deposited into the environment with the feces (Anderson

1963a). Most larvae are found in the mucous coating on the fecal pellets (Forrester and Lankester 1997).

Free-living larvae (L1s) penetrate the foot of a terrestrial snail or slug, and in several weeks develop through a second-stage to the third-stage (L3s) that are infective for definitive hosts (Anderson 1963a). WTD, or other ungulates, become infected by accidentally ingesting gastropods infected with L3s (Lankester and Anderson 1968). Larvae leave the gastropod during the digestion process, penetrate the wall of the abomasum, enter the body cavity and move to the spinal cord (Anderson and Strelive 1967). Approximately 1.5 months after infection, subadult worms migrate up the spinal cord to the cranium where they become sexually mature (Anderson 1963a). The life cycle in a WTD in experimental studies, depending on the dose of larvae administered, can be completed in 3 months (Anderson 1963a).

Parelaphostrongylus tenuis is benign in WTD, but causes fatal neurological disease in many other ungulates. Signs exhibited include: loss of fear, blindness, holding the head to one side, walking aimlessly or in circles, weakness in the hindquarters progressively leading to complete paralysis, and eventually death (Anderson 1965, Carpenter *et al.* 1973, Olsen and Woolf 1978). Wild Cervidae reported with *P. tenuis* infections include: caribou (*Rangifer tarandus terraenovae*) (Bergerud and Mercer 1989), reindeer (Anderson 1970), black-tailed deer (*Odocoileus hemionus columbianus*) (Nettles *et al.* 1977b), fallow deer (*Dama dama*) (Nettles *et al.* 1977a), red deer (*Cervus elaphus*) (Woolf *et al.* 1977) (presumptive), elk (*Cervus elaphus*) (Carpenter *et al.* 1973), and moose (Smith *et al.* 1964, Anderson 1965, Loken *et al.* 1965, Smith and Archibald 1967, Gilbert 1974). Experimentally infected ungulates that show signs of parelaphostrongylosis include: moose (Anderson 1964), caribou (Anderson and Strelive 1968), elk (Samuel *et al.* 1992), mule deer (*Odocoileus hemionus hemionus*) (Anderson *et al.* 1966, Tyler *et al.* 1980), fallow deer (Pybus *et al.* 1992), bighorn sheep (*Ovis canadensis*) (Pybus *et al.* 1996), pronghorn antelope (*Antilocapra americana*) (Tyler and Hibler, unpublished in Anderson and Prestwood 1981), llama (*Lama glama*) (Foreyt *et al.* 1991, Rickard *et al.* 1994), domestic sheep (Anderson and Strelive 1966), and domestic goats (Anderson and Strelive 1972). Captive species (*i.e.*, those that live in zoos or large fenced areas) reported with neurological disease caused by *P. tenuis* include: elk (Olsen and Woolf 1978), eland (*Taurotragus oryx*) (Prestwood, unpublished in Anderson and Prestwood 1981), sable antelope (*Hippotragus niger*) (Nichols *et al.* 1986), reindeer (*Rangifer tarandus tarandus*) (Nichols *et al.* 1986), guanaco (*Lama* *guanacoe*) (Brown *et al.* 1978), bongo (*Tragelaphus eurycerus*) (Nichols *et al.* 1986) (presumptive), scimitar-horned oryx (*Oryx dammah*) (Nichols *et al.* 1986) (presumptive), llama (Brown *et al.* 1978, Baumgartner *et al.* 1985, Krogdahl *et al.* 1987), domestic sheep (Jortner *et al.* 1985), domestic goat (Kopcha *et al.* 1989), and recently a domestic cow (Yamini *et al.* 1997).

Parelaphostrongylus tenuis can be, and often is, fatally pathogenic for individuals of certain species of ungulates. Based on reports of major die-offs in the wild, or susceptibility of hosts experimentally infected with few meningeal worm larvae, the following hosts are quite vulnerable to parelaphostrongylosis: llamas (Foreyt *et al.* 1991, Rickard *et al.* 1994), caribou (Anderson and Strelive 1968, Dauphine 1975) or reindeer (Anderson 1971), mule and black-tailed deer (Tyler *et al.* 1980, Nettles *et al.* 1977b), fallow deer (Pybus *et al.* 1992), elk (Woolf *et al.* 1977, Olsen and Woolf 1978, Samuel *et al.* 1992), and moose (Anderson 1964, 1965).

When the relationship between deer and neurological disease in moose became evident (Anderson 1964), it was proposed that *P. tenuis* may have been the cause for historical declines in several populations of moose (Telfer 1967, Karns 1967, Anderson 1972, Gilbert 1973, Anderson and Prestwood 1981, Lankester 1987). This idea was criticized (Nudds 1990), debated (Gilbert 1992, Nudds 1992), and re-examined by Whitlaw and Lankester (1994). Whitlaw and Lankester (1994) reviewed 80 years of historical data on moose numbers from six areas where moose were sympatric with deer. They found that moose declines were associated with deer densities greater than 5/km^2, but could not separate the role of *P. tenuis* from other mortality-causing factors such as weather, predation, other diseases, or competition for resources. They concluded that, although there is no evidence that *P. tenuis* alone causes moose numbers to decline, it probably limits growth of moose populations that are sympatric with infected deer.

Distribution of *Parelaphostrongylus tenuis*

Parelaphostrongylus tenuis occurs in WTD of eastern North America throughout the deciduous forest biome and deciduous-coniferous ecotone (Anderson 1972) encompassing 27 states of the central and eastern United States and 6 provinces of central and eastern Canada (Figure 1-1). The western-most recovery of adult worms from WTD are from eastern Saskatchewan (Wasel 1995), central North Dakota (Wasel 1995), and eastern Oklahoma (Kocan *et al.* 1982). *P. tenuis* has not been reported West of the great plains

(Bindernagel and Anderson 1972, Samuel and Holmes 1974, Kocan *et al.* 1982, Foreyt and Compton 1991). Western-most distribution is likely influenced by temperature and precipitation (Wasel 1995) that influence numbers and distribution of intermediate hosts that require adequate moisture (Boycott 1934, Baker 1958), and survival of L1s that are sensitive to extreme temperatures and drought (Shostak and Samuel 1984). Some soil types may be inhospitable to intermediate hosts (Burch 1955) and L1s, also accounting for the absence of *P. tenuis* in certain areas (Maze and Johnstone 1986, Platt 1989).

Gastropods as Intermediate Hosts of *Parelaphostrongylus tenuis*

Deer, moose, elk and other ungulates acquire *P. tenuis* by eating infected snails and slugs, the intermediate hosts. Twenty-four species of terrestrial gastropods are known hosts for *P. tenuis* (Table 1-1). A few of these species, however, may be more important for transmission because of their wide-distributions and higher prevalence of infections. *Deroceras laeve*, a slug, and snails, *Zonitoides* spp., *Triodopsis* spp. and *Discus* spp., are among the most widely distributed, abundant and infected gastropods studied (Lankester and Anderson 1968, Maze and Johnstone 1986, Upshall *et al.* 1986, Rowley *et al.* 1987, Platt 1989).

Similar species of gastropods serve as intermediate hosts for nematodes related to *P. tenuis* (*i.e.*, those of the family Protostrongylidae) in areas west of the Great Plains, where *P. tenuis* does not occur. *Deroceras laeve*, *Zonitoides arboreus* and *Zonitoides nitidus*, and *Discus cronkhitei* were among seven species of intermediate hosts for *Parelaphostrongylus odocoilei*, a muscleworm of mule deer, in Jasper National Park, Alberta (Samuel *et al.* 1985). *Discus cronkhitei* was one of 12 known intermediate hosts of *Protostrongylus stilesi* and *Protostrongylus rushi*, lungworms of bighorn sheep (*Ovis canadensis*) of southwestern Alberta (Robb and Samuel 1990). This suggests that if *P. tenuis* were introduced west of the Great Plains, appropriate intermediate hosts would be available to ensure the establishment of the nematode in western populations of ungulate hosts.

Intermediate hosts become infected by crawling on or near ungulate feces infected with first-stage spine-tailed larvae (L1s). Therefore, anywhere large numbers of ungulate hosts congregate and deposit multiple pellet groups, transmission to gastropods should be high. This suggests that focal areas for transmission potentially occur in nature.

Various habitat types have been suggested as potential foci for transmission of *P. tenuis*. Lankester and Anderson (1968) suggest that on Navy Island, Ontario, low, damp, forested habitat, where deer dispersed during the day and where infected gastropods were most common, could serve as foci for transmission, although these areas may be very localized and generally difficult to locate. Kearney and Gilbert (1978) suggested that habitat with white birch (*Betula paperifera*) as a constituent species, could serve as high potential transmission areas because of greater use by both moose and deer and because gastropods were abundant there. Upshall *et al.* (1986) supported this idea and along with Raskevitz *et al.* (1991) suggested that, hardwood dominated habitats serve as areas of potentially high transmission for similar reasons.

More recently Lankester and Peterson (1996) reported higher prevalence of *P. tenuis* in gastropods in a traditional deer wintering yard in Minnesota than on summer range. Surprisingly, very few infected gastropods were discovered, 10 of 12,096 examined. Similarly, Whitlaw *et al.* (1996) found none of 5,917 and 4 of 4,426 gastropods infected with *P. tenuis* larvae collected from New Brunswick summer and winter ranges of WTD, respectively. Results of these studies suggest that deer yards as focal areas might play a relatively minor role in transmission, contrary to expectations, and should be examined more closely.

Reintroduction of Large Ungulates into Former Ranges of Eastern North America

Many state and provincial game agencies of eastern North America have considered reintroducing moose, elk, or caribou onto historic former ranges (Dunn 1965, Dauphine 1975, Severinghaus and Jackson 1970, Allen *et al.* 1987, Schmitt and Aho 1988, Parker 1990, Pitt and Jordan 1994). Meningeal worm plays a major role in each decision to reintroduce these sensitive species to former ranges now occupied by WTD (Severinghaus and Jackson 1970, Lankester and Fong 1989, Parker 1990, Pitt and Jordan 1994). Mortality caused by meningeal worm has been implicated in the failure of a number of translocations throughout North America including an attempt to reintroduce caribou into Nova Scotia in 1968 and 1969 (Dauphine 1975). Three of 51 introduced caribou were observed with signs of neurological disease, and despite reproductive success during the first year, by 1972 the entire herd disappeared (Dauphine 1975). Because there was no evidence of starvation, predation, or poaching, it was assumed that meningeal worm killed the caribou (Dauphine 1975).

Bergerud and Mercer (1989) reviewed 33 introductions of caribou in North America; of these, 20 resulted in sustainable populations and 13 failed. Six of the attempts that failed were in areas where WTD were common. They concluded that in four of the six cases, meningeal worm was the primary factor for the failure, and at least partly responsible, in addition to predation, for the other two failed introductions where deer were present. This included the failed introduction of caribou into Nova Scotia (Dauphine 1975) and a failed introduction of 12 caribou onto an island in Lake Huron, Ontario (Anderson 1972). They also reviewed the failed introduction of 10 caribou from Saskatchewan into Minnesota and translocation of 23 caribou from Newfoundland to Maine (Dunn 1965). Bergerud and Mercer (1989) observed that "Not one caribou introduction succeeded when animals were introduced to ranges where they could make contact with high densities of white-tailed deer infected with meningeal worm." They also concluded that "Caribou introductions will succeed only if spring and summer ranges provide adequate escape cover [from predators] and lack infected gastropods."

Elk reintroductions have been marginally successful; the herds survive but usually in smaller numbers than expected (Carpenter *et al.* 1973, Woolf *et al.* 1977, Eveland *et al.* 1979, Raskevitz *et al.* 1991). A total of 24 elk were relocated from Jackson Hole, Wyoming to indigenous habitat in the northern portion of the lower peninsula of Michigan in 1915 (Moran 1973). Later, sick elk were sighted with signs of blindness, loss of appetite, and loss of fear (Failing 1951). Failing (1951) thought that cobalt deficiency may have been the cause, but evidence was provided by Fay and Stuht (1973) that neurological disease caused by meningeal worm was responsible for clinical signs observed because: 1) 39 elk had been observed with neurological disease since 1938, 2) signs of the disease such as impaired vision, walking aimlessly or in circles, and tilted positioning of the head, fit parelaphostrongylosis, 3) no bacterial or viral agents were isolated, and 4) "since the initial finding [of adult worms in elk] in 1969, meningeal worms are regularly found in neurologically stricken animals."

Between 1969 and 1971, nearly 400 elk were translocated from western Oklahoma, where *P. tenuis* is not found, to areas in eastern Oklahoma where *P. tenuis* is enzootic (Carpenter *et al.* 1973). Five areas of eastern Oklahoma were managed extensively for the translocated elk, but only one area has achieved an increasing population (Raskevitz *et al.* 1991). Despite management efforts, population growth has been slow and *P. tenuis* is thought to be the primary cause of failure in four of the five areas managed for elk (Raskevitz *et al.* 1991). Elk reintroduced to northcentral Pennsylvania in the 1920s have also struggled (Eveland *et al.* 1979), with the population growing from 40 in 1974 (Devlin and Drake 1989) to only 205 in 1993 (Cogan 1993, cited by Thorne *et al.*, manuscript accepted). Despite slow population growth for that herd, more elk were translocated to a small research preserve in western Pennsylvania in 1959 (Woolf *et al.* 1977). Elk numbers never met expectations there either, peaking at 70 animals by the mid 1970s. Olsen and Woolf (1978) concluded that because *P. tenuis* causes death more often in elk calves than in adult elk, population growth would be severely limited.

Everywhere in eastern North America where elk have been reintroduced into areas with infected WTD, some elk have died. For more details on the influence of meningeal worm on elk populations, see Thorne *et al.* (manuscript accepted).

It appears that both elk and caribou populations are often limited by *P. tenuis* and the same is probably true for moose. In fact, it was proposed that *P. tenuis* caused historical declines in moose populations in various locations throughout northeastern North America (Telfer 1967, Karns 1967, Anderson 1972, Gilbert 1973, Prescott 1974). This theory has since been debated (Nudds 1990, Gilbert 1992, Nudds 1992) and reviewed (Whitlaw and Lankester 1994) because moose, deer and meningeal worm have coexisted in Maine (Gilbert 1973, 1974), Minnesota (Karns 1967), New Brunswick (Upshall *et al.* 1987), Nova Scotia (Thomas and Dodds 1988), and Ontario (Anderson 1965, 1972).

Only two state game agencies, the Department of Natural Resources in New York (Severinghaus and Jackson 1970) and the Michigan Department of Natural Resources (MDNR) (Hicke 1943, Schmitt and Aho 1988) have attempted to reintroduce moose within the distribution of *P. tenuis*. Small numbers of moose were reintroduced into the Adirondacks of New York between 1894 and 1903, but the attempt failed to establish a viable population (Severinghaus and Jackson 1970). In light of the historical failure and the current population size of deer known to be infected with meningeal worm (Behrend 1970), Severinghaus and Jackson (1970) concluded that "...the evidence indicates strongly that [neurological disease] would doom any stocking effort to failure". Consequently, no further efforts have been made to reestablish moose in the state of New York.

The first attempts in 1934 and 1937, to reintroduce 71 moose from Isle Royale, Michigan, into eastern parts of Michigan's upper peninsula also failed. A second attempt was made in 1985 and 1987 when 61 moose from Algonquin Provincial Park, Ontario, were reintroduced into the western region of Michigan's upper peninsula. Results of this reintroduction are still being evaluated, but it appears that moose numbers are much lower than expected (MDNR 1997b).

Wisconsin also considered reintroducing moose but habitat limitations coupled with the threat of meningeal worm eliminated that option (Parker 1990). An alternative strategy was proposed to manage areas of northern Wisconsin to foster survival of the few moose that wander in from the neighboring states of Minnesota and Michigan (Parker 1990).

Although meningeal worm alone may not cause all reintroductions of cervids to fail, evidence strongly suggests that *P. tenuis* will probably limit population growth for elk, moose, and caribou in areas sympatric with infected WTD (Anderson 1972, Olsen and Woolf 1978, Whitlaw and Lankester 1994). It is also evident that caribou are more sensitive to *P. tenuis* infection (Anderson and Strelive 1968, Bergerud and Mercer 1989) than either elk or moose, therefore, caribou should not be introduced anywhere *P. tenuis* is found in WTD.

History of White-tailed Deer in Michigan's Upper Peninsula

Historically, Michigan's upper peninsula was at the northern edge of WTD range (Baker 1983). WTD are found most abundantly where low-growing, dense vegetation offers adequate food and cover (Harlow 1984). These favorable conditions are associated with early successional stages of forest growth created naturally by fire and windthrow, or by the manual clearing of land through logging or farming (Blouch 1984). Until 1840 very little suitable habitat existed for WTD among the large undisturbed stands of virgin timber of Michigan's upper peninsula (Bartlett 1938). Logging of large red pine (*Pinus resinosa*) and eastern white pine (*Pinus strobus*) in the central area of northern Michigan began on a commercial basis around 1838 (Langhorne 1988; cited by Van Deelen *et al.* 1996). It was then that WTD expanded their summer range northward and numbers were high by 1890 (Bartlett 1938).

During winters WTD congregated in dense stands of lowland conifer ("yards") comprised of northern white-cedar (*Thuja occidentalis*) and eastern hemlock (*Tsuga canadensis*) predominantly. These areas offered adequate shelter from wind, cold, and deep snow, but provided very limited amounts of food (Verme 1965, Van Deelen *et al.* 1996). Deer must have traveled to nearby upland stands for food and withdrew into the conifers during adverse weather (Ozoga and Gysel 1972). The first destruction of swamp-conifer wintering areas for deer took place around 1900, with clear-cut harvest of eastern hemlock and northern white cedar, as well as hardwoods (Bartlett 1938). This resulted in frequent slash fires and grasses progressively replaced preferred browse species for deer. In response, deer numbers decreased and remained low until around 1920, when fire suppression resulted in recovery of browse species (Bartlett 1938, Jenkins and Bartlett 1959).

In 1921 the "buck law" became effective and only antlered deer could be taken by hunters (Langenau 1994). Also, large-scale logging continued in swamp areas of conifer, and tree tops were left behind to feed deer through winter. Numbers of deer began to increase dramatically as more does survived winters (Bartlett 1938). By 1928, virgin timber was depleted, lumbering decreased, and deer that had been nurtured beyond winter carrying capacity, starved (Bartlett 1950). By the 1930's importance of winter habitat (yarding areas) was clearly recognized and logging strategies that could benefit deer were discussed (Aldous 1941, Verme 1965). At the same time long term effects of the "buck law" were questioned by wildlife managers (Langenau 1994).

Systematic survey for determining deer numbers in the upper peninsula was initiated in 1932 by counting numbers of deer/100 hours of time spent in the field (Bartlett 1938). In 1935, deer drives were conducted to attempt to drive out and count all deer in a square mile area. In 1940, 89 drives were conducted and densities averaged 15 deer/mi^2 (= 5.8/km^2) or approximately 240,000 deer (Doepker *et al.* 1994).

Deer numbers peaked by autumn 1949 at 630,000 animals (MDNR 1996) and began another decline as overbrowsed deer yards became death traps and nutritionally stressed does that did survive produced few young (Jenkins and Bartlett 1959, Langenau 1994). In 1956 the first antlerless deer hunting since the 1920s occurred in Michigan's upper peninsula despite opposition from the public (Langenau 1994). This followed discovery of 74,000 dead deer that died in the winter of 1955 (Jenkins and Bartlett 1959). By fall 1960 the total population for the northern peninsula was an estimated 329,000, an average of 7.7/km^2 (MDNR 1996).

Habitat for deer declined steadily between 1940 and 1960, partly due to overbrowsing and partly due to forest succession as timber matured and less ground-level vegetation was available for deer to eat (Langenau 1994). By the mid 1970s the estimated density of deer in autumn was as low as 1.2/km^2 (Blouch 1984), the lowest since the 1800s (Bartlett 1938). Plans to improve deer range were developed in the 1970s, including strategies to improve winter habitat (Johnston 1975). In addition, government funding was designated for the cultivation and maintenance of thousands of hectares of forest openings (Langenau 1994). Increased timber markets and more agriculture in the upper peninsula also aided habitat improvement for deer, but recovery was slow (Langenau 1994).

Deer numbers began to increase again in the 1980s. Some mild winters and increased timber production that facilitated supplemental feeding of deer through winters (Rob Aho, personal communication) resulted in a rapid increase in deer numbers over a 6 year period from 370,000 (8.6/km^2) in autumn 1983 to 608,000 (14.2/km^2) in autumn 1988 (Hill 1994). By autumn 1993, numbers of deer reached an all time recorded high of nearly 740,000 with an average overall density of 17.4/km^2 (Hill 1994). It was only a matter of time before another "crash" in the WTD population occurred. In fact, two consecutive severe winters in 1995 and 1996 reduced deer numbers dramatically. About 8.8 m and 9.9 m of snow fell during the winters of 1995-96 and 1996-97 respectively. The spring estimate of numbers of deer for 1997 was 366,000 deer in the upper peninsula (MDNR 1997a).

History of Moose in Michigan's Upper Peninsula

Moose were native to Michigan's upper peninsula (Baker 1983). The earliest account was in 1652 by a trapper named Radisson who described hunting Oriniacks (Indian name for moose) near the mouth of the Huron River that flows into Huron Bay (Hicke 1943). Although unsure of the source, Hicke (1943) also states that in 1661 at L'Anse "one report reads, 'The savages were living on moose meat, which came very opportunely.'" Another trapper who lived in the upper peninsula between 1748 and 1793 also noted that "'This region still abounds, but less so than formerly, in bear, moose, beaver, otter, marten, and muskrat'" (Hicke 1943).

By 1860, however, sightings of moose were rare (Hicke 1943). Moose seemed to disappear from the western end of the peninsula but remained in the eastern portion. Several moose had been seen or killed after 1864 in counties of the eastern upper peninsula (Hicke 1943). In 1889, legislation was granted for complete legal protection of moose (Hicke 1943). A yearling cow was killed in Mackinac County in July 1899 and the violators were prosecuted (Hicke 1943). By 1943, 13 more dead moose were discovered showing that some moose still lived in the eastern part of Michigan's upper peninsula (Hicke 1943).

Isle Royale, an island of Michigan in Lake Superior, was known to have a moose population of at least 200 as of 1916 (Hicke 1943). As an island vacation resort, hands-off management was applied and numbers of moose grew to between 1000 and 2000 animals by 1930 (Hicke 1943). In winter of 1934, large numbers of moose died of starvation, inspiring a list of management options that included live trapping and transport to the northern peninsula of Michigan (Hicke 1943).

Trapping of moose on Isle Royale took place between 1934 and 1937; a total of 71 moose were translocated to the upper peninsula in Cusino, Keweenaw, and Escanaba River Tract areas (Hicke 1943). Reasoning behind the reintroduction was to remove surplus moose from Isle Royale in a humane manner, and to re-establish a viable population in the northern peninsula (Hicke 1943). It was considered an experimental project in hope for success despite that few moose lingered in the eastern portion of the peninsula or that unfavorable factors such as roads, towns, and increased numbers of hunters were present (Hicke 1943). The experimental release however, failed to establish a larger self-sustaining population probably because of high numbers of deer and poaching (Schmitt and Aho 1988, Aho and Hendrickson 1989).

A second reintroduction took place in 1985 and 1987, again in hopes to establish a viable population. Sixty-one moose were translocated from Algonquin Provincial Park to Marquette County in Michigan's upper peninsula (Figure 1-2) and mortality-sensing radio-collars were fitted on them all (Schmitt and Aho 1988). Forty-one additional moose, born and captured in the same area in the upper peninsula between 1989 - 1995, were also radio-collared.

The estimated population in 1989 in the western half of the peninsula was 124 moose with an average calf survival, through their first winter, of 82% (Aho and Hendrickson 1989). Between 1985 and 1997, meningeal worm was attributed as the cause of mortality in 17 of 53 (32%) moose examined (MDNR 1997d). Other deaths were diagnosed as fetal complications with birthing, liver flukes, hepatitis and peritonitis, and various injuries (Aho and Hendrickson 1989).

In 1991, aerial censuses conducted on radio-collared moose between January and March indicated a population of 210 moose, from which was projected a postpartum population of 273 moose (Aho 1995). By 1994, based on calf production and aerial censuses, two population models estimated 304 or 334 moose living in the western portion of the peninsula (Aho 1995).

A total moose count was attempted during February and March 1997, which included the primary range of translocated moose. Biologists flying seven aerial survey plots, each averaging 23 mi^2 (59.6 km^2), counted every moose they saw (MDNR 1997b). However, precision was poor and few moose were visible, the mean estimated number was 107 ± 103 standard error (MDNR 1997b). It was thought that harsh winter conditions limited visibility for locating moose that remained sheltered under conifers, or that crusted snow may have impeded ability to detect moose tracks (Robert Aho, personal communication). Because moose use heavy cover during late winter, Phillips *et al.* (1973) suggested aerial counts be conducted during early winter (December - January) when weather conditions allow. Therefore, another total moose count was conducted during the mild winter of 1997-98; only 120 moose (± 44) were observed (Rob Aho, personal communication) which is much lower than originally predicted by population models.

There is a small population of moose still living in the eastern half of the upper peninsula (Munising to Sault Ste. Marie) comprised of a remnant indigenous population, immigrants from Ontario, and progeny from the 1934 - 1937 translocation from Isle Royale (Aho 1995). There were 71 recorded sightings of moose between October 1996 and July 1997 (MDNR 1997c). Only one moose from the 1985 and 1987 translocation is known to have migrated to the eastern half of the peninsula, but others probably have (Aho 1995). Three moose were diagnosed with meningeal worm as the cause of death from the eastern half of the peninsula since 1985 (Steve Schmitt, personal communication).

Rationale, Objectives and Hypotheses

This thesis deals with the ecology of meningeal worm, *Parelaphostrongylus tenuis*, in gastropod intermediate hosts, and definitive hosts WTD and moose in Baraga County of Michigan's upper peninsula. Field work was done from May 1995 to August 1996. The study was prompted by the following actions, discoveries and conjectures:

(1) reintroduction of 61 moose to Michigan's upper peninsula in 1985 and 1987 by the Michigan Department of Natural Resources in hopes to reestablish a viable population;

(2) subsequent death of some of these animals attributed to meningeal worm;

(3) increasing numbers of WTD, the usual host for meningeal worm;

(4) little is known about transmission of *P. tenuis*, particularly aspects related to overlapping populations of definitive (WTD and moose) and intermediate (gastropod) hosts, and;

(5) the opinions by personnel of the Michigan Department of Natural Resources that meningeal worm might negatively affect the long-term success of the moose reintroduction program.

Moose numbers in the upper peninsula appeared to be increasing steadily since the reintroductions of 1985 and 1987 (Aho 1995). Population surveys of the moose in 1997 (MDNR 1997b) and 1998 (Rob Aho, personal communication), however, indicate that numbers of moose are not nearly as high as predicted by population models. This suggests, at the least, that more information on *P. tenuis* in Michigan's upper peninsula is essential. I attempted to determine whether one or several factors, such as seasonal distribution of definitive hosts, or distribution of infected gastropods, could result in increased exposure of moose to this parasite.

Some objectives dealt with WTD to determine the current status of *P. tenuis* within the resident population during the time of this study. Prevalence of meningeal worm in Michigan, based on examination of deer heads for adult worms, had not been done since DeGuisti's surveys in the 1950s and early 1960s (DeGuisti 1955, 1963). Therefore, I examined deer heads collected from various counties throughout the upper peninsula. The following hypotheses were tested:

> **Ho**: Population size of adult *P. tenuis* is similar among deer of different geographic location, age, and gender, within Michigan's upper peninsula, **Ha**: Population size of adult *P. tenuis* varies between location, age, and gender within Michigan's upper peninsula.

I thought that deer would have variable numbers of L1s in their feces throughout the year, based on literature for related protostrongylid nematodes and a recent paper on *P. tenuis* (Peterson *et al.* 1996). Therefore, I collected deer feces opportunistically for one year and examined pellet groups for intensity of spine-tailed larvae to test the following hypotheses:

> **Ho**: Shedding of L1s in feces of WTD does not differ by month throughout the year, and **Ha**: Shedding of L1s in feces of WTD fluctuates seasonally in accord with findings for other related nematodes.

Protostrongylid nematodes related to *P. tenuis*, (*i.e.*, the muscleworm, *Parelaphostrongylus andersoni*, and the lungworm, *Varestrongylus alpenae*) may be present in WTD of the upper peninsula (Dikmans 1934, Pybus *et al.* 1990). These closely related parasites have dorsal-spined L1s similar to those of *P. tenuis*. Misidentified L1s could confound prevalence data based on spine-tailed larvae in feces. I attempted to locate adult *P. andersoni* in muscles of WTD and larval stages of *V. alpenae* from feces. Larval stages of *V. alpenae* are shorter than those of *P. tenuis* (Gray *et al.* 1985) so I measured lengths of L1s. The following hypotheses were tested:

Ho: Meningeal worm is the only protostrogylid nematode in WTD and gastropods of Michigan's upper peninsula, **Ha**: Other related worms such as *P. andersoni* and *Varestrongylus alpenae* occur in WTD and gastropods of Michigan's upper peninsula.

Little is known about the ecology of gastropods in the upper peninsula, much less their role as intermediate hosts for *P. tenuis*. Thus, my final objectives were 1) to determine species abundance and distribution of terrestrial gastropods and look for broad habitat types that appear more suitable than others for gastropods, 2) to determine which species were most often infected with *P. tenuis* larvae, and 3) to examine the idea of foci of infection (*i.e.*, to determine if infected gastropods occur in high densities in areas/habitats frequented by deer or moose). The following hypotheses were tested:

H1o: Densities of gastropods will be random across varying habitats and disturbed areas, **H1a**: Densities of gastropods will vary greatly according to habitat and human disturbance.

H2o: Many species of gastropods will be infected naturally with *P. tenuis*, **H2a**: Few species of gastropods will be infected naturally with *P. tenuis* larvae.

H3o: Infected gastropods will be randomly distributed throughout areas inhabited by deer or moose. **H3a**: Densities of infected gastropods will vary greatly between areas inhabited by deer or moose.

Study Area

Baraga County was selected as the study area because it 1) encompasses a large portion of the primary range of translocated moose, 2) has a large sympatric population of white-tailed deer with associated yarding areas, and 3) has accessible public lands. Originally, Marquette County was to be included for similar reasons, but logistics of collections and funding capabilities eliminated this option.

Baraga County is 2,333 km^2 and borders 105 km of shoreline of Lake Superior in Michigan's upper peninsula (Berndt 1988) (Figure 1-3). It has a cool climate with mean daily temperatures 15 - 20°C in July and -15 to -10°C in January (Barrett *et al.* 1995). Snowfall can occur as early as September and often falls through April, with greater occurrence at higher elevations away from the lake (Barrett *et al.* 1995). The average annual precipitation between April and September is 54 cm (Berndt 1988). The average seasonal snowfall is approximately 360 cm, with higher amounts at higher elevations (Berndt 1988).

Topography ranges from gently sloping and nearly level outwash plains, to steep ridges and extrusive hills (Berndt 1988). The highest points in Michigan are located in the eastern part of Baraga County where Mount Arvon and Mount Curwood reach elevations of approximately 604 m above sea level (Berndt 1988) (Figure 1-4).

There are three main divisions of bedrock in Baraga County: 1) lower Precambrian rocks, mainly granite and gneiss outcrops located in the eastern elevations of the Peshekee Uplands, 2) middle Precambrian, mainly slate and associated rocks of the northeastern, central, and southern portions of the county, and 3) Precambrian sandstone underlying the northern parts (Berndt 1988).

The dominant forest communities are northern hardwoods of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and basswood (*Tilia americana*), and hardwood/conifer mix that includes the mentioned deciduous species plus balsam fir (*Abies balsamea*), eastern hemlock, and eastern white pine (*Pinus strobus*) (Barnes and Wagner 1981, Landsat Imagery Map 1991). Spruce-fir communities are scattered throughout the county and are found in larger contiguous patches in the center and south-central area (Landsat Imagery Map 1991). These areas include species such as black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir, tamarack (*Larix laracina*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*) (Barnes and Wagner 1981). Interspersed amongst these conifer-dominated areas and widely scattered throughout the county are hundreds of small pockets of poorly drained lowland hardwoods and conifer bog-swamp communities that often include black ash (*Fraxinus nigra*) and grade into a northern deciduous-conifer swamp community (Barnes and Wagner 1981) of previously mentioned species.

There is a flat, sandy area dominated by planted jack pine (*Pinus banksiana*), larger pockets of red pine (*Pinus resinosa*), eastern white pine, and herbaceous shrubland known as the Baraga Outwash Plains in the western portion of the county (Landsat Imagery Map 1991) (Figure 1-4). Limited by the short growing season, most agricultural land is located in the northeastern sections of the Sturgeon River Valley and South of the Baraga Outwash Plains (Landsat Imagery Map 1991). Only 3% of land is classified as farmland, while 91% remains forested (Berndt 1988).

Baraga County has about 1,080 lakes that range in size from 2 ha to 326 ha (Berndt 1988). There are 1024 km of streams and rivers that flow northward to Lake Superior with a few in the southern portion that flow southward towards Lake Michigan (Berndt 1988). Most of the riverbeds have rocky substrate and waterfalls are common. The longest, Sturgeon River (129 km), leaves the northwestern part of the county as a broad meandering river with a wide flood plain (Berndt 1988).

Table 1-1. Known intermediate hosts of *Parelaphostrongylus tenuis*. Gastropod classification after Burch and Pearce, 1990 (From Thorne et. al, manuscript accepted).

- Phyllum Mollusca
- Class Gastropoda
- Subclass Prosobranchia (=Streptonsura)
    - Order Archaeogastropods
        - Suborder Neritopsina
            - Family Helicinidae
                - *Helicina orbiculata*
- Subclass Pulmonata
    - Order Geophila (= Stylommatophora)
        - Suborder Orthurathra
            - Family Cionellidae (= Cochliocopidae)
                - *Cionella lubrica*
                - *Cionella* spp.
        - Suborder Sigmurethra
            - Family Discidae
                - *Anguispira alternata*
                - *Discus cronkhitei*
                - *Discus patulus*
            - Family Phylomycidae
                - *Pallifera dorsalis*
                - *Philomycus carolinianus*
            - Family Arionidae
                - *Arion circumscriptus*
            - Family Vitrinidae (= Zonitoidae)
                - *Mesomphix cupreus*
                - *Nesovitrea electrina*
                - *Zonitoides (Ventridens) collisella*
                - *Zonitoides (Z.) arboreus*
                - *Zonitoides (Z.) nitidus*
            - Family Limacidae
                - *Deroceras laeve*
                - *Deroceras reticulatum*
            - Family Mesodontidae (= Polygyridae)
                - *Mesodon (Inflectarius) inflectus*
                - *Polygyra dorfeuilliana*
                - *Polygyra jacksoni*
                - *Stenotrema fraternum*
                - *Stenotrema stenotrema*
                - *Triodopsis (Neohelix) albolabris*
                - *Triodopsis divesta*
                - *Triodopsis tridentata*

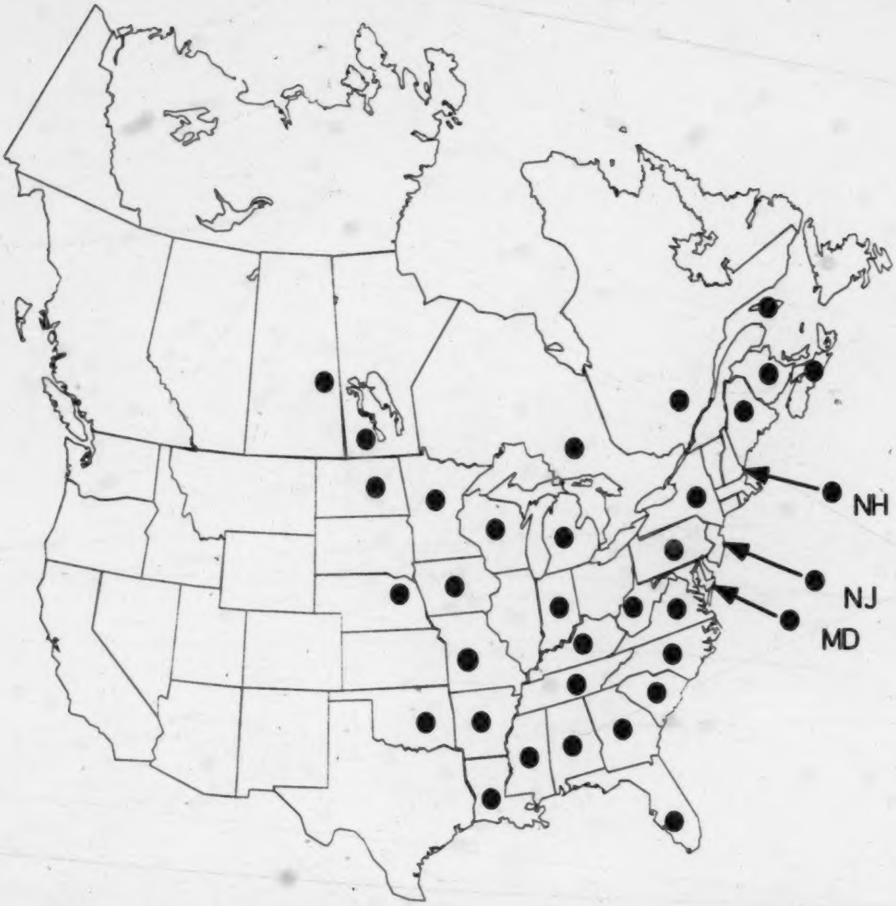

Figure 1-1. Provinces and states where *Parelaphostrongylus tenuis* was found in white-tailed deer (after Wasel 1995). Based on data from Samuel (1969), Anderson and Prestwood (1981), Beaulieu-Goudreault (1981), Garrison *et al.* (1987), Upshall *et al.* (1987), Thomas and Dodds (1988), Platt (1989), Foreyt and Compton (1991), Comer *et al.* (1991), Jarvinen and Hedberg (1993), and Oates (1997, personal communication).

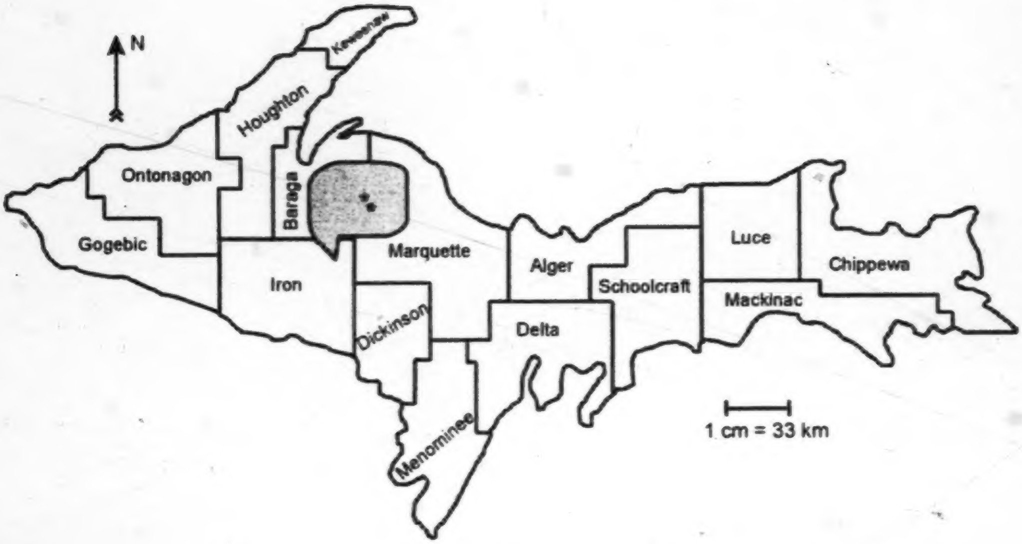
N
Keweenaw
Houghton
Ontonagon
Baraga
Gogebic
Iron
Marquette
Alger
Schoolcraft
Luce
Chippewa
Mackinac
Delta
Dickinson
Menominee
1 cm = 33 km

Figure 1-2. Release sites* of moose translocated from Ontario in 1985 and 1987 to Michigan's upper peninsula. Shaded area shows the core region occupied by translocated moose and offspring (after Aho 1995).

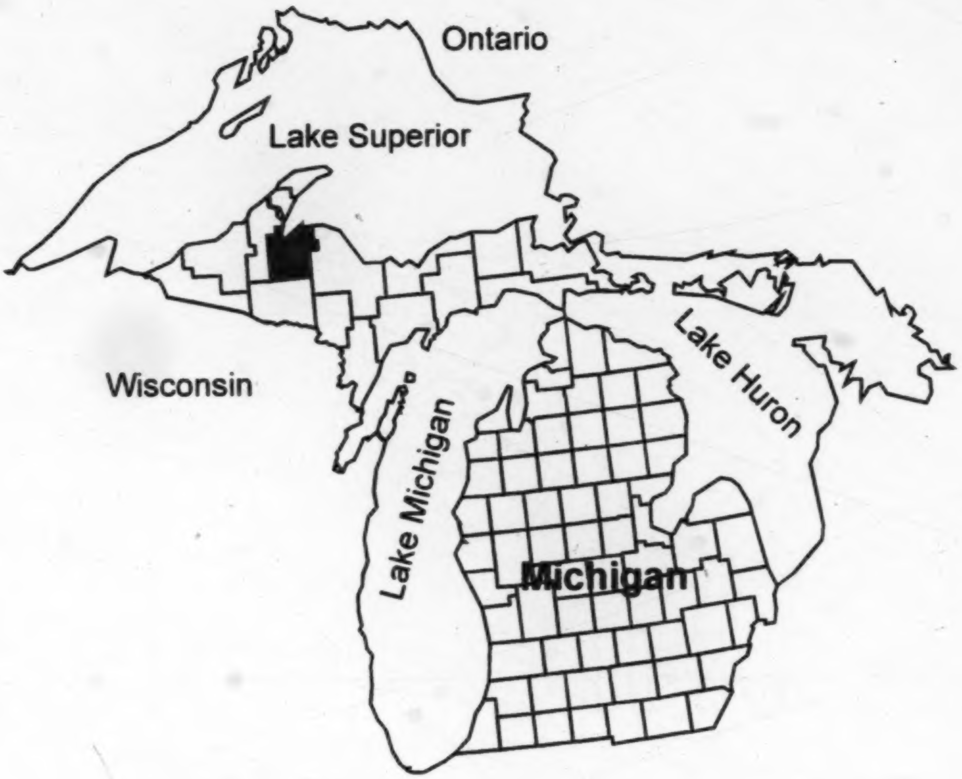
Ontario
Lake Superior
Wisconsin
Lake Michigan
Lake Huron
Michigan

Figure 1-3. Location of the study area, Baraga County of Michigan's upper peninsula.

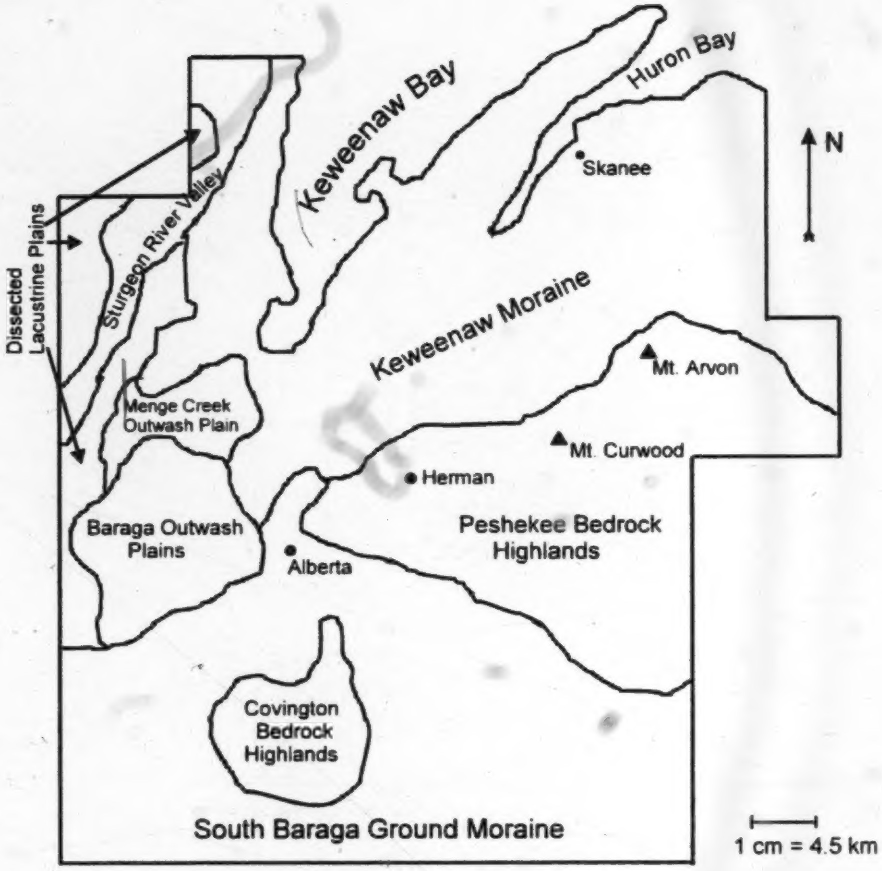
Keweenaw Bay
Huron Bay
N
Skanee
Dissected Lacustrine Plains
Sturgeon River Valley
Keweenaw Moraine
Mt. Arvon
Menge Creek Outwash Plain
Mt. Curwood
Herman
Baraga Outwash Plains
Alberta
Peshekee Bedrock Highlands
Covington Bedrock Highlands
South Baraga Ground Moraine
1 cm = 4.5 km

Figure 1-4. Physiographic regions of Baraga County with landmarks (after Berndt 1988 and Barrett *et al.* 1995).

Literature Cited

Aho, R.W. 1995. Michigan's translocated moose population: 10 years later. Michigan Department of Natural Resources Wildlife Division Report Number 3245. 18 pp.

Aho, R.W. and J. Hendrickson. 1989. Reproduction and mortality of moose translocated from Ontario to Michigan. Alces 25: 75-80.

Aldous, S.E. 1941. Deer management suggestions for the northern Michigan white cedar type. The Journal of Wildlife Management 5: 90-94.

Allen, A.W., P.A. Jordan, and J.W. Terrell. 1987. Habitat suitability model: moose (Lake Superior region). United States Department of Interior, U.S. Fish and Wildlife Service, Biological Report 82(10.155). 47 pp.

Anderson, R. C. 1963a. The incidence, development, and experimental transmission of *Pneumostrongylus tenuis* Dougherty (Metastrongyloidea: Protostrongylidae) of the meninges of white-tailed deer (*Odocoileus virginianus borealis*) in Ontario. Canadian Journal of Zoology 41: 775-792.

-------- 1963b. Studies on *Pneumostrongylus tenuis* Dougherty, 1945 of *Odocoileus virginianus*. The Journal of Parasitology 49: 47.

-------- 1964. Neurologic disease in moose infected experimentally with *Pnuemostrongylus tenuis* from white-tailed deer. Pathologia Veterinaria. 1: 289-322.

-------- 1965. An examination of wild moose exhibiting neurologic signs, in Ontario. Canadian Journal of Zoology 43: 635-639.

-------- 1970. The ecological relationships of meningeal worm (*Pneumostrongylus tenuis* Dougherty, 1945) and native cervids in North America. (Abstract) The Journal of Parasitology (Section 2, Part 1) 56(4), (Proceedings of the 2nd International Congress of Parasitology, Washington D.C.) pp. 6-7.

-------- 1971. Neurologic disease in reindeer (*Rangifer tarandus tarandus*) introduced into Ontario. Canadian Journal of Zoology 49: 159-166.

-------- 1972. The ecological relationships of meningeal worm and native cervids in North America. Journal of Wildlife Diseases 8: 304-310.

Anderson, R. C. and M. W. Lankester. 1974. Infectious and parasitic diseases and arthropod pests of moose in North America. Le Naturaliste Canadien 101:23-50.

Anderson, R. C. and A. K. Prestwood. 1981. Lungworms. Pages 266 - 317 *In* Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.), Diseases and parasites of white-tailed deer. Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida. 458 pp.

Anderson, R. C. and U. R. Strelive. 1966. Experimental cerebrospinal nematodiasis (*Pnuemostrongylus tenuis*) in sheep. Canadian Journal of Zoology 44: 889-894.

-------- and --------. 1967. The penetration of *Pnuemostrongylus tenuis* into the tissues of white-tailed deer. Canadian Journal Zoology 45: 285-289.

-------- and --------. 1968. The experimental transmission of Pneumostrongylus tenuis to caribou (Rangifer tarandus terraenovae). Canadian Journal of Zoology 46: 503-510.

-------- and --------. 1972. Experimental cerebrospinal nematodiasis in kids. The Journal of Parasitology 58:816.

Anderson, R. C., M.W. Lankester, and U.R. Strelive. 1966. Further experimental studies of *Pneumostrongylus tenuis* in cervids. Canadian Journal of Zoology 44: 851-861.

Baker, H.B. 1958. Land snail dispersal. The Nautilus 71: 141-148.

Baker, R. 1983. Mammals of Michigan. Wayne State University Press, Detroit, Michigan. 642 pp.

Barnes, B.V. and W.H. Wagner, Jr. 1981. Michigan trees. The University of Michigan Press, Ann Arbor. 383 pp.

Barrett, L.R., J. Liebens, D.G. Brown, R.J. Schaetzl, P. Zuwerink, T.W. Cate, and D.S. Nolan. 1995. Relationships between soils and presettlement forests in Baraga County, Michigan. American Midland Naturalist 134: 264-285.

Bartlett, I.H. 1938. Michigan's deer problem. (Bulletin) Michigan Department of Conservation, Lansing, Michigan. 64 pp.

-------- 1950. Michigan deer. (Bulletin) Michigan Department of Conservation, Lansing, Michigan. 11 pp.

Baumgartner, W., A.M. Zajac, B.L. Hull, F. Andrews, and F. Garry. 1985. Parelaphostrongylosis in llamas. Journal of American Veterinary and Medical Association 187: 1243-1245.

Beaulieu-Goudreault, M. 1981. Etude des endoparasites et plus specialement du ver des meninges (Parelaphostrongylus tenuis) du cerf de virginie (Odocoileus virginianus) a l'ile d'Anticosti. M.Sc. Thesis, Institute of Parasitology, University McGill, Montreal. 65 pp.

Behrend, D.F. 1970. The nematode, *Pneumostrongylus tenuis*, in white-tailed deer in the Adirondacks. New York Fish and Game Journal 17: 45-49.

Bergerud, A.T. and W.B. Mercer. 1989. Caribou introductions in eastern North America. Wildlife Society Bulletin 17: 111-120.

Berndt, L.W. 1988. Soil survey of Baraga County area, Michigan. United States Department of Agriculture, Washington D.C. 306 pp.

Bindernagel, J.A. and R.C. Anderson. 1972. Distribution of meningeal worm in white-tailed deer in Canada. The Journal of Wildlife Management 36: 1349-1353.

Blouch, R.I. 1984. Northern great lakes states and Ontario forests. Pages 391-410 *In* L.K. Halls (ed.), White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania. 870 pp.

Boycott, A.E. 1934. The habitats of land mollusca in Britain. Journal of Ecology 22: 1-38.

Brown, T.T., Jr., H.E. Jordan, and C.N. Demorest. 1978. Cerebrospinal parelaphostrongylosis in llamas. Journal of Wildlife Diseases 14: 441-444.

Burch, J.B. 1955. Some ecological factors of the soil affecting the distribution and abundance of land snails in eastern Virginia. The Nautilus 69: 62-68.

Carpenter, J.W., H.E. Jordan, and B.C. Ward. 1973. Neurologic disease in wapiti naturally infected with meningeal worms. Journal of Wildlife Diseases 9: 148-153.

Cogan, R. 1993. Elk population survey. Annual Project Report. Pennsylvania Game Commission, Bureau of Wildlife Management, Research Division, Harrisburg. 12 pp.

Comer, J.A., W.R. Davidson, A.K. Prestwood, and V.F. Nettles. 1991. An update on the distribution of *Parelaphostrongylus tenuis* in the southeastern United States. Journal of Wildlife Diseases 27: 348-354.

Dauphine, T.C. Jr. 1975. The disappearance of caribou reintroduced to Cape Breton Highlands National Park. The Canadian Field-Naturalist 89: 299-310.

DeGuisti, D.L. 1955. The occurrence of a protostrongylid nematode in the meninges of Michigan deer. The Journal of Parasitology 41(2):42 (abstract).

-------- 1963. Incidence and distribution of *Elaphostrongylus odocoilei* in Michigan deer herd. The Journal of Parasitology 49(Supplement): 47.

Devlin, D. and W. Drake. 1989. Pennsylvania elk census - 1989. Annual Unpublished Report. Pennsylvania Game Commission, Harrisburg, Pennsylvania. 8 pp.

Doepker, R.V., D.E. Beyer, Jr., and M. Donovan. 1994. Deer population trends in Michigan's upper peninsula. Michigan Department of Natural Resources, Lansing, Michigan. Unpublished Report Number 3254. 11 pp.

Dunn, F.D. 1965. Reintroduction of woodland caribou to Mt. Katahdin, Maine. Transactions of The Northeast Fish and Wildlife Conference 22: 1-5.

Eveland, J.F., J.L. George, N.V. Hunter, D.M. Forney, and R.L. Harrison. 1979. A preliminary evaluation of the ecology of the elk in Pennsylvania. Pages 145-151 *In* M.S. Boyce and L.D. Hayden-Wing (eds.), North American elk: Ecology, behavior and management. University of Wyoming, Laramie.

Failing, O. 1951. Pigeon River elk. Michigan Conservation 20: 4-6, 23.

Fay, L.D. and J.N. Stuht. 1973. Meningeal worm in association with neurologic disease in Michigan wapiti. Annual Conference Wildlife Disease Association, University of Connecticut, Storrs, Connecticut. p. 32.

Foreyt W.J. and B.B. Compton. 1991. Survey for meningeal worm (*Parelaphostrongylus tenuis*) and ear mites in white-tailed deer from northern Idaho. Journal of Wildlife Diseases 27: 716-718.

Foreyt W.J., L.G. Rickard, S. Dowling, S. Parish, and M. Pipas. 1991. Experimental infections of two llamas with the meningeal worm (*Parelaphostrongylus tenuis*). Journal of Zoo and Wildlife Medicine 22: 339-344.

Forrester, S.G. and M.W. Lankester. 1997. Extracting protostrongylid nematode larvae from ungulate feces. Journal of Wildlife Diseases 33: 511-516.

Garrison, R.C., D.C. Ashley, and D.J. Robbins. 1987. The 1986 survey for meningeal worm in white-tailed deer in northwestern Missouri. Transactions of the Missouri Academy of Science 21: 149. (Abstract)

Gilbert, F.F. 1973. *Parelaphostrongylus tenuis* (Dougherty) in Maine: I - The parasite in white-tailed deer (*Odocoileus virginianus*, Zimmerman). Journal of Wildlife Diseases 9: 136-143.

-------- 1974. *Parelaphostrongylus tenuis* in Maine: II - Prevalence in moose. The Journal of Wildlife Management 38: 42-46.

-------- 1992. Retroductive logic and the effects of meningeal worms: a comment. The Journal of Wildlife Management 56: 614-616.

Gleich, J.G., F.F. Gilbert, and N.P. Kutscha. 1977. Nematodes in terrestrial gastropods from central Maine. Journal of Wildlife Diseases 13: 43-46.

Gray, J.B., W.M. Samuel, A.W. Shostak, and M.J. Pybus. 1985. *Varestrongylus alpenae* (Nematoda: Metastrongyloidea) in white-tailed deer (*Odocoileus virginianus*) of Saskatchewan. Canadian Journal of Zoology 63: 1449-1454.

Harlow, R.F. 1984. Habitat evaluation. Pages 601-628 *In* L.K. Halls (ed.), White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania. 870 pp.

Hicke, P.F. 1943. Michigan moose. Michigan Department of Conservation, Lansing, Michigan. 57 pp.

Hill, H.R. 1994. The 1994 deer pellet group surveys. Michigan Department of Natural Resources, Wildlife Division Report Number 3211. 15 pp.

Jarvinen, J.A. and W.A. Hedberg. 1993. *Parelaphostrongylus tenuis* (Nematoda) in white-tailed deer (*Odocoileus virginianus*) in central Iowa. The Journal of Parasitology 79: 116-119.

Jenkins, D.H. and I.H. Bartlett. 1959. Michigan whitetails. Michigan Department of Conservation, Lansing, Michigan. 80 pp.

Johnston, W.F. 1975. Reproducing lowland conifer forests. Journal of Forestry 73:17-20.

Jortner, B.S., H.F. Troutt, T. Collins, and K. Scarratt. 1985. Lesions of spinal cord parelaphostrongylosis in sheep. Sequential changes following intramedullary larval migration. Veterinary Pathology 22: 137-140.

Karns, P.D. 1967. *Parelaphostrongylus tenuis* in deer in Minnesota and implications for moose. The Journal of Wildlife Management 31: 299-303.

Kearney, S.R. and F.F. Gilbert. 1978. Terrestrial gastropods form the Himsworth Game Preserve, Ontario, and their significance in *Parelaphostrongylus tenuis* transmission. Canadian Journal of Zoology 56: 688-694.

Kocan, A.A., M.G. Shaw, K.A. Waldrup, and G.J. Kubat. 1982. Distribution of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) in white-tailed deer from Oklahoma. Journal of Wildlife Diseases 18: 457-460.

Kopcha, M., J.V. Marteniuk, R. Sills, B. Steficek, and T.W. Schillhorn van Veen. 1989. Cerebrospinal nematodiasis in a goat herd. Journal of American Veterinary and Medical Association 194: 1439-1442.

Krogdahl, D.W., J.P. Thilsted, and S.K. Olsen. 1987. Ataxia and hypermetria caused by *Parelaphostrongylus tenuis* infection in llamas. Journal of the American Veterinary and Medical Association 190: 191-193.

Landsat Imagery Map. 1991. Michigan Technological University, Houghton, Michigan.

Langenau, E. 1994. 100 years of deer management in Michigan. Michigan Department of Natural Resources, unpublished report no. 3213. 15 pp.

Langhorne, W.T. 1988. Investigations of the spatial, temporal, and organizational processes of the industrial frontier: a case study from the upper peninsula of Michigan. Ph.D. Thesis, Michigan State University, East Lansing. 331 pp.

Lankester, M.W. 1987. Pests, parasites and diseases of moose (*Alces alces*) in North America. Swedish Wildlife Research Viltrevy, Supplement 1, Part 2: 461-489.

Lankester, M.W. and R.C. Anderson. 1968. Gastropods as intermediate hosts of *Pneumostrongylus tenuis* Dougherty of white-tailed deer. Canadian Journal of Zoology 46:373-383.

Lankester, M.W. and D. Fong. 1989. Distribution of elaphostrongyline nematodes (Metastrongyloidea: Protostrongylidae) in Cervidae and possible effects of moving *Rangifer* spp. into and within North America. Alces: 25: 133-145.

Lankester, M.W. and W.J. Peterson. 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. Journal of Wildlife Diseases 32: 31-38.

Lankester, M.W. and W.M. Samuel. 1997. Pests, parasites and diseases. Pages 479-517 *In* C.C. Schwartz and A.W. Frazmann (eds.), Ecology and Management of the North American Moose. A Wildlife Management Institute Book, Smithsonian Institution Press, Washington D.C. 733 pp.

Loken, K.I., J.C. Schlotthauer, H.J. Kurtz, and P.D. Karns. 1965. *Pneumostrongylus tenuis* in Minnesota moose (*Alces alces*). Wildlife Disease Association Bulletin 1:7.

Maze, R.J. and C. Johnstone. 1986. Gastropod intermediate hosts of the meningeal worm *Parelaphostrongylus tenuis* in Pennsylvania: observations on their ecology. Canadian Journal of Zoology 64: 185-188.

Michigan Department of Natural Resources (MDNR). 1996. 1938-1996 Michigan deer population figures. Unpublished. 1 pp.

-------- 1997a. The 1997 deer pellet group surveys. Unpublished. 1 pp.

-------- 1997b. Result of moose census. Unpublished memo. 5 pp.

-------- 1997c. Moose sightings in eastern upper peninsula of Michigan. Unpublished memo. 1 pp.

-------- 1997d. Moose mortalities examined at the lab 1985 to 1997. Unpublished memo. 3 pp.

Moran, R.J. 1973. The Rocky Mountain elk in Michigan. Michigan Department of Natural Resources, Wildlife Division, Research and Development Report Number 267, Lansing, Michigan. 93 pp.

Nettles, V.F., A.K. Prestwood, and R.D. Smith. 1977a. Cerebrospinal parelaphostrongylosis in fallow deer. Journal of Wildlife Diseases 13: 440-444.

-------- , --------, R.G. Nichols, and C.J. Whitehead. 1977b. Meningeal worm-induced neurologic disease in black-tailed deer. Journal of Wildlife Diseases 13: 137-143.

Nichols, D.K., R.J. Motali, L.G. Phillips, T.P. Alvarado, M. Bush, and L. Collins. 1986. *Parelaphostrongylus tenuis* in captive reindeer and sable antelope. Journal of the American Veterinary and Medical Association 188: 619-621.

Nudds, T.D. 1990. Retroductive logic in retrospect: The ecological effects of meningeal worms. The Journal of Wildlife Management 54: 396-402.

-------- 1992. Retroductive logic and the effects of meningeal worms: a reply. The Journal of Wildlife Management 56: 617-619.

Olsen, A., and A. Woolf. 1978. The development of clinical signs and the population significance of neurological disease in a captive wapiti herd. Journal of Wildlife Diseases 14: 263-268.

Ozoga, J.J. and L.W. Gysel. 1972. Response of white-tailed deer to winter weather. The Journal of Wildlife Management 36: 892-896.

Parker, L.R. 1990. Feasibility assessment for the reintroduction of North American elk, moose, and caribou into Wisconsin. Wisconsin Department of Natural Resources, Bureau of Research. 115 pp.

Peterson, W.J., M.W. Lankester, and M.R. Riggs. 1996. Seasonal and annual changes in shedding of *Parelaphostrongylus tenuis* larvae by white-tailed deer in northeastern Minnesota. Alces 32: 61-73.

Phillips, R.L., W.E. Berg, and D.B. Siniff. 1973. Moose movement patterns and range use in northwestern Minnesota. The Journal of Wildlife Management 37: 266-278.

Pitt, W.C. and P.A. Jordan. 1994. A survey of the nematode parasite, *Parelaphostrongylus tenuis* in the white-tailed deer, *Odocoileus virginianus*, in a region proposed for caribou, *Rangifer tarandus caribou*, re-introduction in Minnesota. The Canadian Field-Naturalist 108: 341-346.

Platt, T.R. 1989. Gastropod intermediate hosts of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) from northwestern Indiana. The Journal of Parasitology 75:519--523.

Prescott, W.H. 1974. Interrelationships of moose and deer of the genus *Odocoileus*. le Naturaliste Canadien 101: 493-504.

Pybus, M.J., S. Groom, and W.M. Samuel. 1996. Meningeal worm in experimentally-infected bighorn and domestic sheep. Journal of Wildlife Diseases 32: 614-618.

Pybus, M.J., W.M. Samuel, D.A. Welch, J. Smits, and J.C. Haigh. 1992. Mortality of fallow deer (*Dama dama*) experimentally infected with meningeal worm, *Parelaphostrongylus tenuis*. Journal of Wildlife Diseases 28: 95-101.

Raskevitz, R.F., A.A. Kocan, and J.H. Shaw. 1991. Gastropod availability and habitat utilization by wapiti and white-tailed deer sympatric on range enzootic for meningeal worm. Journal of Wildlife Diseases 27: 92-101.

Rickard, L.G., B.B. Smith, E.J. Gentz, A.A. Grank, E.G. Pearson, L.L. Walker, and M.J. Pybus. 1994. Experimentally induced meningeal worm (*Parelaphostrongylus tenuis*) infection in the llama (*Llama glama*): Clinical evaluation and implications for parasite translocation. Journal of Zoo Wildlife Medicine 25: 390-402.

Robb, L.A., and W.M. Samuel. 1990. Gastropod intermediate hosts of lungworms (Nematoda: Protostrongylidae) on bighorn sheep winter range: aspects of transmission. Canadian Journal of Zoology 68: 1976-1982.

Rowley, M.A., E.S. Loker, J.F. Pagels, and R.J. Montali. 1987. Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National Zoological Park's Conservation and Research Center, Virginia. Journal of Parasitology 73: 1084-1089.

Samuel, W.M. and J.C. Holmes. 1974. Search for elaphostrongyline parasites in cervids from Alberta. Canadian Journal of Zoology 52: 401-403.

Samuel, W.M., T.R. Platt, and S.M. Knispel-Krause. 1985. Gastropod intermediate hosts and transmission of *Parelaphostrongylus odocoilei*, a muscle-inhabiting nematode of mule deer, *Odocoileus h. hemionus*, in Jasper National Park, Alberta. Canadian Journal of Zoology 63: 928-932.

Samuel, W.M., M.J. Pybus, D.A. Welch, and C.J. Wilke. 1992. Elk as a potential host for meningeal worm: implications for translocation. The Journal of Wildlife Management 56: 629-639.

Schmitt, S.M., and R.W. Aho. 1988. Reintroduction of moose from Ontario to Michigan. Pages 258-274 *In* Nielsen, L., and R.D. Brown (eds.), Translocation of wild animals. Wisconsin Humane Society, Milwaukee and Caesar Kleberg Wildlife Research Institute, Kingville, Texas. 333 pp.

Severinghaus, C.W. and L.W. Jackson. 1970. Feasibility of stocking moose in the Adirondacks. New York Fish and Game Journal 17: 18-32.

Shostak, A.W. and W.M. Samuel. 1984. Moisture and temperature effects on survival and infectivity of first-stage larvae of *Parelaphostrongylus odocoilei* and *P. tenuis* (Nematoda: Metastrongyloidea). The Journal of Parasitology 70: 261-269.

Smith, H.J. and R.M. Archibald. 1967. Moose sickness, a neurological disease of moose infected with the common cervine parasite, *Elaphostrongylus tenuis*. Canadian Veterinary Journal 8: 173-177.

Smith, H.J., R.M. Archibald, and A.H. Comer. 1964. Elaphostrongylosis in maritime moose and deer. Canadian Veterinary Journal 5: 287-296.

Telfer, E.S. 1967. Comparison of moose and deer winter range in Nova Scotia. The Journal of Wildlife Management 31: 418-425.

Thomas, J.E. and D.G. Dodds. 1988. Brainworm, *Parelaphostrongylus tenuis*, in moose, *Alces alces*, and white-tailed deer, *Odocoileus virginianus*, of Nova Scotia. Canadian Field Naturalist 102: 639-642.

Thorne, E.T., E.S. Williams, W.M. Samuel, and T.P. Kistner. Diseases and parasites. *In*: D.E. Toweill and J. W. Thomas (eds.), Elk of North America: Ecology and Management (2nd Edition). Stackpole Books, Mechanicsberg, Pennsylvania. (Manuscript accepted; 152 manuscript pages.)

Tyler, G.V., C.P. Hibler, and A.K. Prestwood. 1980. Experimental infection of mule deer with *Parelaphostrongylus tenuis*. Journal of Wildlife Diseases 16: 533-540.

Upshall, S.M., M.D.B. Burt, and T.G. Dilworth. 1986. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in terrestrial gastropods. Journal of Wildlife Diseases 22: 582-585.

--------, --------, and --------. 1987. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). Journal of Wildlife Diseases 23:

Van Deelen, T.R., K.S. Pregitzer, and J.B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. The American Midland Naturalist 135: 181-194.

Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan. Journal of Forestry 63: 523-529.

Wasel, S.M. 1995. Meningeal worm, *Parelaphostrongylus tenuis* (Nematoda), in Manitoba, Saskatchewan, and North Dakota: Distribution and ecological correlates. M.Sc. Thesis, Department of Zoology, University of Alberta, Edmonton. 100 pp.

Whitlaw, H.A., and M.W. Lankester. 1994. A retrospective evaluation of the effects of parelaphostrongylosis on moose. Canadian Journal of Zoology 72: 1-7.

Whitlaw, H.A., M.W. Lankester, and W.B. Ballard. 1996. Parelaphostrongylus tenuis in terrestrial gastropods from white-tailed deer winter and summer range in northern New Brunswick. Alces 32: 75-83.

Woolf, A., C.A. Mason, and D. Kradel. 1977. Prevalence and effects of *Parelaphostrongylus tenuis* in a captive wapiti population. Journal of Wildlife Diseases 13: 149-154.

Yamini, B., J.C. Baker, P.C. Stromberg, and C.H. Gardiner. 1997. Cerebrospinal nematodiasis and vertebral chondrodysplasia in a calf. Journal of Veterinary Diagnostic Investigation 9: 451-454.

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CHAPTER II. PREVALENCE AND INTENSITY OF *PARELAPHOSTRONGYLUS TENUIS* IN WHITE-TAILED DEER

Introduction

Meningeal worm, *Parelaphostrongylus tenuis*, is a parasitic nematode commonly found in the cranial cavities of its natural host, white-tailed deer (*Odocoileus virginianus*) (WTD). Deer exhibit few signs of infection but *P. tenuis* causes severe, often fatal, neurologic disease in other ungulates, including moose (*Alces alces*) (Anderson 1972). A variety of terrestrial snails and slugs serve as intermediate hosts. Gastropods become infected with first-stage (L1s) larvae deposited into the environment on the fecal pellets of WTD. Ungulate hosts, deer and moose, acquire the infection by accidentally eating infected gastropods.

The presence of *P. tenuis* is monitored in WTD by determining prevalence within the population, often by locating adult worms in the cranium (Smith *et al.* 1964, Karns 1967, Behrend and Witter 1968, Behrend 1970, Carpenter *et al.* 1973, Gilbert 1973, Pursglove 1977, Dew 1988). DeGuisti (1955) offered the first prevalence data for *P. tenuis* in Michigan's upper peninsula by locating adult worms. Many studies base identification of the nematode on presence of dorsal-spined larvae (L1s) in feces rather than locating adults in heads (Samuel and Beaudoin 1966, Saunders 1973, Schmitt *et al.* 1989, Peterson and Lankester 1991, Whitlaw and Lankester 1994, Peterson *et al.* 1996). However, this method is not specific for *P. tenuis* because other parasitic nematodes are known to shed dorsal-spined L1s in feces of WTD. Two such parasites, *Parelaphostrongylus andersoni* (a muscleworm) and *Varestrongylus alpenae* (a lungworm), have been reported from deer in Michigan's upper peninsula (Dikmans 1934, Pybus *et al.* 1990). Therefore, determining prevalence of L1s in feces may overestimate numbers of WTD infected with *P. tenuis*.

Moose were recently reintroduced to Michigan's upper peninsula in 1985 and 1987; some have succumbed to *P. tenuis*-induced neurologic disease. Risk for moose to acquire meningeal worm depends on the distribution of infected gastropods in the environment. Although there is little information on the ecology of gastropods in Michigan's upper peninsula, in general, gastropods are abundant in many habitat types (Baker 1958, Clarke *et al.* 1968). Therefore, one might predict that the distribution of infected gastropods depends on patterns of habitat use by WTD.

In the upper peninsula, WTD are widely distributed throughout varying habitats most of the year. In winter, however, deer migrate to lower elevations along Lake Superior. They congregate in large numbers typically in lowland conifer forests known as "yards" and stay throughout the winter. They often center on logged areas or artificial feeding areas which occur in various habitat types.

Deer in winter yards deposit huge numbers of larvae in small areas. Results of recent studies have shown that numbers of L1s in feces is highest during late-winter and early-spring (Peterson *et al.* 1996) when deer may still remain in yards. If gastropods are present where the L1s are concentrated, this creates potential foci of infected gastropods. These foci, depending on the circumstances, could be beneficial for sympatric moose if they are in areas that moose avoid. On the contrary, some areas could be potential "hot spots" for transmission if ungulate hosts frequent them during snow-free seasons and infected gastropods are available to be ingested.

Determination of prevalence with *P. tenuis* infection in WTD of Michigan's upper peninsula, by locating adult worms in heads, had not been done since Deguisti's study in 1955. At the time of my study, numbers of WTD were high (MDNR 1996), therefore, status of *P. tenuis* in WTD could have implications for sympatric moose. Seasonal output of larvae in particular, could affect distributions of infected gastropods and subsequent transmission to moose. In addition, parasites related to *P. tenuis* (*P. andersoni* and *V. alpenae*) may be present in deer of Michigan's upper peninsula; their presence had not been confirmed recently in naturally infected WTD. The following hypotheses were tested:

> **Ho**: Population size of adult *P. tenuis* is similar among deer of different geographic location, age, and gender, within Michigan's upper peninsula, **Ha**: Population size of adult *P. tenuis* varies between location, age, and gender within Michigan's upper peninsula.
>
>> Given the abundance of published information on this subject, and the relative homogeneity of the landscape in Michigan's upper peninsula, I predicted that the population size would not differ by geographic location or host gender, but would differ by host age.

Ho: Shedding of L1s in feces of WTD does not differ by month throughout the year, and **Ha**: Shedding of L1s in feces of WTD fluctuates seasonally in accord with findings for other related nematodes.

> Based on previous findings, I predicted that numbers of dorsal-spined L1s in deer feces would peak in late winter-early spring, thus providing maximum exposure to gastropods that overwintered in these areas, and to young gastropods hatched from eggs during summer.

Ho: Meningeal worm is the only protostrogylid nematode in WTD and gastropods of Michigan's upper peninsula, **Ha**: Other related worms such as *P. andersoni* and *Varestrongylus alpenae* occur in WTD and gastropods of Michigan's upper peninsula.

> The widespread distribution of *P. andersoni* and *V. alpenae* in WTD and previous reports in deer from Michigan's upper peninsula, indicate that such parasites would be present.

Methods

Search for Adult *Parelaphostrongylus tenuis* in Heads of White-tailed Deer

A total 216 deer heads was collected from various counties in the upper peninsula. July 1995 through December 1995 heads were collected from deer killed on roads, and through November and December 1995 from meat processing plants and check stations during and after firearm hunting season. Heads were stored frozen at approximately -20 C until January 1997 at which time they were transferred to a field station owned by Michigan Technological University, Ford Forestry Center (also known as Alberta location), L'Anse, Michigan, where they were stored frozen outdoors for approximately 2 weeks.

Frozen heads were cut sagitally using a band saw. Fifty-eight heads damaged by trauma or in a state of advanced decay were discarded. Heads (n = 158) were thawed a minimum of 12 hrs at approximately 20 C. Deer were aged according to tooth eruption and relative tooth wear as described by Severinghaus (1949) and placed in three general categories: fawns (less than 1 year old), yearlings (1-2 years old) and adults (2.5 years old and older). Brain hemispheres were removed and the cavernous, intercavernous, transverse and sagittal blood sinuses, along with the inner surface of the dura were examined for adult worms (Prestwood and Smith 1969). Cranial cavities were rinsed and re-examined; water rinsings were examined for adult worms. Worms were carefully collected using small forceps and stored in 10% glycerin alcohol. Age, sex, county of collection if known, and number of worms found per deer were recorded. Number of worms was estimated grossly if extracted singly, or examined at 50X using a dissecting microscope to count tail ends of tangled worms.

Numbers of infected animals were compared by age class, by sex, and by county using G-tests (Zar 1984). Intensity of infections was compared by age class, by sex, and by county using Kruskal-Wallis one-way analyses of variance. Statistics were calculated using the Statistical Package for the Social Sciences (SPSS). Results were considered significant at $P \leq 0.05$.

Search for Dorsal-spined Larvae in Feces of White-tailed Deer

Fecal pellet groups (218 total) from WTD were collected opportunistically between 21 June 1995 and 30 May 1996. Pellets were collected fresh when either defecation was witnessed, or pellets were still moist or if pellets were frozen in winter. Numbers of samples ranged from 3 to 18 per month. The entire pellet group was collected and all pellet groups were stored individually, frozen, and examined within five months of collection.

Approximately 20 gm (range 13.6 to 25.7 gm) per pellet group were examined for dorsal-spined larvae, based on Mason's (1989) suggested optimum sample mass of 8 – 20 gm. Pellets were processed using a modified Baermann technique (Samuel and Gray 1982). Pellets were weighed, wrapped in double-layered cheese-cloth, and allowed to stand 24 hr in 650 ml water in clean, plastic, 20 cm funnels. One hundred ml of the solution were drained into two 50 ml test tubes and centrifuged at 1500 rpm approximately 10 min. The top 30 ml were discarded and the two samples combined by rinsing one sample into the other with 10 ml of fresh water and centrifuged 10 min. The top 30 ml were removed and the remaining 20 ml solution rinsed into 6 cm plastic petri dishes with grids etched into the bottom. Dorsal-spined larvae, both live and dead, were observed using a dissecting microscope at 25X and counted at least twice. Larvae were counted repeatedly until two consecutive totals differed < 10%. Counts were averaged for the total number of larvae. Number of larvae were reported as larvae per gram (lpg) of fecal pellets.

To avoid contamination between pellet groups, funnels were cleaned with soap and hot water while being scrubbed with a bottle brush, rinsed with 95% ethanol, and rinsed again with hot tap water. Plastic petri dishes were cleaned in the same manner. The bottle brush was washed similarly and allowed to soak in a 15% bleach solution, for over 24 hrs, between trials. Funnels were tested for contamination, at random, by setting up Baermann funnels containing plain water, processing them the same as fecal pellet solutions and examining for larvae. No larvae were recovered from cleaned Baermann apparati (n = 25).

Prevalence of infection was compared by month and by season using G-tests (Zar 1984). Using SPSS statistical software, data were tested for normal distribution using Kolmogrov-Smirnov test, and for heterogeneity of variance using Levine's test. Numbers of lpg were compared between months and seasons using a one-way ANOVA on log transformed data. Tukey's Honestly-Significant-Difference post-hoc test was used to determine which months and which seasons differed from each other (Zar 1984). Results were considered significant at $P \leq 0.05$. Legally designated climatological seasons were used as time periods when calculating seasonal data.

Search for Adult *Parelaphostrongylus andersoni* in Muscles of White-tailed Deer

Based on a suggested minimum sample size by Prestwood *et al.* (1974), five entire backstraps (longissimus dorsi muscles) and one hindquarter from WTD were examined for adult muscleworm using methods described by Prestwood (1972) and Pybus and Samuel (1984). Specimens were collected from five dead deer, either hit by vehicles or that died in winter. Entire muscles were examined grossly for hemorrhagic areas and carefully teased apart with a sharp point. The tissue was then sliced thinly and examined for lesions and worms using a lighted magnifier (2X) and by closer examination using a dissecting microscope (5X to 25X).

Two specimens had extensive head trauma and so only three of the five deer were examined for adult *P. tenuis* . Feces of all five deer were examined for dorsal-spined larvae.

Results

Search for Adult *Parelaphostrongylus tenuis* in Heads of White-tailed Deer

Sixty-nine of 158 (44%) deer examined were found infected with adult worms. Baraga, Iron, and Marquette counties, where translocated moose and offspring were known to inhabit, had slightly, but not significantly, lower prevalences than other counties ($G = 13.4$, $P > 0.10$) (Table 2-1). Intensity of infection varied between counties, but differences were not significant ($H = 16.7$, $P = 0.06$). Overall, number of worms per deer ranged from 1 to 5, with a mean intensity of 1.7 (± 1.1) worms. Of 69 infected deer, 40 had single worms in the cranium.

Fifty-three of 124 (43%) female deer, and 16 of 34 (47%) male deer were infected ($G = 0.20$, $P > 0.50$). Intensity of infection between the sexes was not different ($H = 0.04$, $P = 0.85$).

Prevalence of infection was significantly lower in fawns ($G = 8.3$, $P < 0.025$), than in yearlings or adults. Fawns also had significantly fewer worms ($H = 12.6$, $P = 0.002$) than older age classes (Table 2-2). All infected fawns had a single worm.

Search for Dorsal-spined Larvae in Feces of White-tailed Deer

Sixty-three percent (137/218) of deer pellet groups were infected with dorsal-spined larvae. Prevalence of these larvae, which were either those of *P. tenuis* or close relatives, did not fluctuate by season ($G = 2.05$, $P \leq 0.6$) (Table 2-3). Larvae per gram of feces differed significantly by season ($F = 12.5$, $P < 0.001$) with peak numbers in spring (Figure 2-1). More larvae were deposited during winter and spring than summer and autumn. One pellet group with exceptionally high numbers of larvae (946 lpg) was collected 30 May 1996. This outlier was removed from calculations of intensity to represent better natural occurrences. Significant comparisons were maintained even without it.

Larvae per gram were significantly different when compared by month ($F = 5.7$, $P < 0.001$). The highest numbers of larvae occurred in May (omitting the outlier), and lowest numbers in November (Figure 2-2). Greatest numbers of larvae were deposited February through May, significantly more than July, October, or November.

Two sizes of L1s were present in a few fecal samples examined suggesting that *V. alpenae* was present (Gray *et al.* 1985). Size differences between L1s were only detectable when both sizes were present as reference for comparison. I attempted to measure some of the smaller larvae, however, they were preserved in the same manner as living L3 larvae in hot alcohol heated by microwave (see page 63). Many specimens were coiled making accurate measurements difficult, therefore, this study offers only anecdotal evidence that smaller larvae presumably from *V. alpenae* were present in WTD.

Search for Adult *Parelaphostrongylus andersoni* in Muscles of White-tailed Deer

No adult muscleworms were found in five deer examined (Table 2-4). Several small areas of hemorrhage were detected in the backstraps and two small areas in the hindquarter but no worms were recovered upon closer inspection. One deer, an adult female killed on a road and collected February 1997, had dorsal-spined larvae in the feces. The head was not examined due to damage caused by trauma. No other deer examined had larvae in feces or adult worms in the head.

Discussion

Results from this study were consistent with the pattern of larval shedding reported previously for *P. tenuis* (Peterson *et al.* 1996) and related protostrongylid nematodes (Uhazy *et al.* 1973, Samuel *et al.* 1985). Peak numbers of *P. tenuis* L1s were found between February and May in feces of WTD in Minnesota (Peterson *et al.* 1996). High numbers of L1s for *Parelaphostrongylus odocoilei* in mule deer of Alberta occured in March and April (Samuel *et al.* 1985). Peak numbers were found between January and April for *Protostrongylus* spp. in bighorn sheep of western Alberta and eastern British Columbia (Uhazy *et al.* 1973). High numbers of L1s during late winter-early spring often overlaps with the time of year that WTD of northern latitudes congregate in wintering areas known as "yards", particularly during harsh winters.

In Michigan's upper peninsula, deer migrate toward lower elevations along the edge of Lake Superior where they stay throughout winter. They often concentrate in areas where logging takes place. Logging in the upper peninsula occurs mainly in mixed conifer-deciduous stands in winter and is mostly a selective-cutting method rather than clear-cut in Baraga County (personal observation). Selective-cutting leaves trees behind as shelter for daytime bedding sites, at the same time offers downed tops of trees as supplemental feed for deer. Yards are usually within range of a dense conifer stand where deer sleep at night, but they spend most of the day in feeding areas around fallen tops of trees, or in artificial feeding areas supplied by local residents.

'Traditional', naturally-occurring yards common in the upper peninsula in earlier decades were comprised almost entirely of swamp-conifer tree species and selected for protection from chilling winds and deep snowfall (Van Deelen *et al.* 1996) rather than availability of food. Despite critically low browse availability, deer would return to these same conifer stands annually for many years until the stand lost its ability to maintain a stable microclimate (Verme 1965).

Deer yards created by selective logging have greater potential for creating foci for transmission than historically natural occurring yards for three reasons: 1) concentrations of deer change locations with logging operations, therefore, deer may be lured into areas they normally would not select under natural conditions, 2) downed trees and slash left behind from selective logging may enhance habitat for terrestrial gastropods by offering food and shelter (Boycott 1934, Gleich and Gilbert 1973), and 3) regrowth of succulent vegetation facilitated by openings in the canopy may attract ungulates to the logged areas during snow free periods (*i.e.*, when infected gastropods are available for ingestion).

To illustrate better the potential for deer yards to become focal areas for infection, the following is a presumptive calculation of dorsal-spined larvae potentially deposited in deer yards. For example, adult, free-ranging, female WTD in northeastern Minnesota defecated an average of 22 times per day, January through April (Rogers 1987). I weighed 19 pellet groups (gm, wet weight), presumably from adult, female deer on my study area between January and April, and found an average 62.2 gm (± 7.7 s.d.) of feces per pellet group. So, in general, an adult, female WTD defecates approximately 1370 gm of feces per day. Using the average larvae per gram (65.5 lpg, ± 81.2 s.d.) that I found for that same time period in the upper peninsula, WTD shed approximately 90,000 larvae per day between January and April. Thus, one infected deer in Michigan's upper peninsula could, and probably does, shed several million larvae (actually, 10.8 million larvae using the aforementioned estimates) between January and April. If gastropods are present in the areas where deer concentrate, and definitive hosts use these areas during snow-free seasons, the potential for transmission is obviously quite high.

During severe winters, deer in the upper peninsula may remain in yards as late as early May. This did not occur in the western portion of the upper peninsula in winter 1994-95 but did occur in winters, 1995-96 and 1996-97 (personal observation). Therefore, except during harsh winters, deer are probably leaving the yards when L1s in feces reach peak numbers. When 'traditional' deer yards were used, exodus probably occurred earlier even during harsh winters, because a food source was unavailable. I believe this was a selective advantage for the parasite to distribute large numbers of L1s and promote infection of gastropods over large areas. Because ingestion of infected gastropods occurs by chance (Anderson 1972), it seems advantageous to have smaller numbers of infected gastropods scattered widely, rather than large numbers of gastropods localized in small areas that may be overlooked by passing ungulates during snow-free seasons.

Other advantages for *P. tenuis* to increase output of larvae with the onset of spring is that it probably allows better survival of free-living L1s because of high moisture (Shostak and Samuel 1984). Spring also coincides with the emergence of terrestrial gastropods that serve as intermediate hosts. Subsequent transmission of L1s to gastropods during spring probably ensures that infective L3s will be available by autumn, which coincides with the weaning of fawns. So, at least some fawns will become infected within their first year as seen in the upper peninsula (this study), northeastern Minnesota (Peterson and Lankester 1991, Slomke *et al.* 1995, Peterson *et al.* 1996) and elsewhere.

Lankester (1987) suggests that the barometer of success of *P. tenuis* in reaching new hosts should be reflected by changes of prevalence in fawns. Yarding behaviour of WTD probably causes a majority of a majority of the L1s to be concentrated in localized areas, thus limiting the distribution of infected gastropods. In years when the preceding winter was harsh, lower prevalence in fawns could result because of the limited distribution of L1s in the environment. Some studies examined successive, annual, prevalence in fawns, but few found dramatic differences between years. Prevalence in fawns from Maine was 44%, 53%, and 42% in 1968, 1969, and 1970, respectively (Gilbert 1973); prevalence in fawns from Rachelwood Wildlife Preserve in western Pennsylvania was 53%, 11%, 76%, and 70% in 1972, 1973, 1974, and 1975, respectively (David R. Anderson, personal communication). Prevalence in fawns from Maine was 66% and 23% in 1988 and 1989, respectively (Bogaczyk *et al.* 1993); prevalence in fawns of southeastern Manitoba was 10% and 11% in 1989 and 1990, respectively (Wasel 1995). Anderson's (personal communication) results from Pennsylvania and Bogaczyk *et al.*'s (1993) results from Maine suggest that prevalence in fawns may serve as a "barometer" of potential transmission to ungulates, particularly between years of extreme climatic differences.

Bogaczyk *et al.* (1993) suggests that "The unusually dry and somewhat cooler July conditions may have slowed the development of larvae in gastropods, resulting in reduced prevalence of fawns born in 1989. Also, July weather could have forced gastropods to aestivate, reducing their likelihood of being ingested by deer." None of the studies considered previous winter weather but lower prevalence, in some cases, may have resulted from previous harsh winter conditions that kept deer in yards longer and limited the dispersal of L1s. This theory remains only speculative because I did not have timely access to weather data from Pennsylvania or Maine to explore this potential phenomenon in further detail.

Prevalence is most often determined by locating adults in heads or by locating dorsal-spined larvae in feces, but few studies have looked at both consecutively in the same deer. A few studies that have (Bogaczyk *et al.* 1993, Slomke *et al.* 1995) found higher prevalence of infection with *P. tenuis* by locating adults in heads rather than finding dorsal-spined larvae with feces. Bogaczyk *et al.* (1993) and Slomke *et al.* (1995) concluded that this was because of single worm or single sex infections in WTD. All fawns in the present study had single worm infections. Bogaczyk *et al.* (1993) found 9% of WTD in Maine had single worm infections, but did not specify age classes. They did, however, find significantly lower mean intensity of infection in fawns than older deer, so most of the single worm infections were probably in fawns. Slomke *et al.* (1995) found greater numbers of single sex infections in fawns, although they didn't specify how many were single worms or several worms of single sex.

Studies where deer were examined concurrently for adults and L1s, reported the following combinations: single worms present and larvae absent (Bogaczyk *et al.* 1993), multiple worms of single sex present and larvae absent (Slomke *et al.* 1995), worms of both sex present and larvae absent (Slomke *et al.* 1995), worms of both sex present and larvae present (Slomke *et al.* 1995), and multiple worms of unknown sex present and larvae absent (Garner and Porter 1991, Bogaczyk *et al.* 1993), and no worms detected but larvae present (Anderson 1963, Samuel and Beaudoin 1966, Garner and Porter 1991, Bogaczyk *et al.* 1993). These findings suggest that if *P. tenuis* is the only protostrongylid parasite present in the WTD populations studied, finding adult worms in heads would consistently reveal higher prevalence than locating larvae in feces.

However, many studies that look at prevalence of larvae in feces and prevalence of adults in heads, examine them from different deer during similar time periods. Results from these studies show consistently higher prevalence of dorsal-spined larvae in feces (Anderson 1963, Garner and Porter 1991, Bindernagel and Anderson 1972, Thomas and Dodds 1988). I also found higher prevalence of larvae in feces than adults in heads. It is possible that adult worms located in the spinal column were overlooked and/or that some feces may have been collected repeatedly from some of the same deer. However, it is more likely that closely related parasites such as *Parelaphostrongylus andersoni* or *Varestrongylus alpenae* with similar looking dorsal-spined L1s to those of *P. tenuis* are present in the WTD.

Garner and Porter (1991) examined WTD in New York for *P. tenuis,* and recognized the possibility of related worms being present. They did not find adult *P. andersoni* in 56 partial loin muscles examined. Bogaczyk *et al.* (1993) also considered the possibility that worms related to *P. tenuis* were probably present in WTD of Maine. They found no adult *P. andersoni* in three longissimus dorsi muscles even though the deer examined had larvae present in feces and no adult *P. tenuis*. Another study in Maine (Bogaczyk 1992) found no adult *P. andersoni* in 42 longissimus dorsi muscles examined.

Adult *P. andersoni* have not been found in deer of Michigan's upper peninsula either, although they probably occur there. Pybus *et al.* (1990) recovered adult *P. andersoni* from a WTD experimentally infected with L3s that originated from a "pooled" collection of deer feces, some from Michigan's upper peninsula, and some from a small area in western Pennsylvania. Nine other animals, experimentally infected with larvae collected solely fro m the same small area in Pennsylvania, harbored only *P. tenuis*. This led Pybus *et al.* (1990) to conclude that *P. andersoni* came from the Michigan portion of the feces. However, Prestwood *et al.* (1974) have shown that few WTD are naturally infected with both *P. andersoni* and *P. tenuis*. This suggests that cross-immunity might be involved. If so, the adult *P. andersoni* found in the Pybus *et al.* (1990) study could still have come from Pennsylvania.

Known distribution of *P. andersoni* is disjunct but wide-ranging, from five states in the southeastern United States (Prestwood *et al.* 1974) and New Jersey (Pursglove 1977), to central regions of the Northwest Territories (in caribou) (Lankester and Hauta 1989), to northeastern Wyoming (Edwards 1995), in southeastern British Columbia (Pybus and Samuel 1981) and probably in Michigan (Pybus *et al.* 1990). Because of its broad distribution between very different climatic regions, *P. andersoni* is probably more widespread than currently realized (Anderson and Prestwood 1981, Pybus and Samuel 1981). Prestwood *et al.* (1974) suggested a minimum sample size of five deer to detect presence or absence, but five may be too few if prevalence of the parasite is very low (Anderson and Prestwood 1981) or if the examiner(s) is inexperienced at locating the small worm in muscle.

Varestrongylus alpenae occurs in lungs of WTD. It is a very difficult worm to locate because of its small size, cryptic location, and lack of lesions in vicinity of the worms (Prestwood and Pursglove 1974, Anderson and Prestwood 1981, Gray *et al.* 1985). Dikmans (1934) originally described *V. alpenae* from specimens collected in Michigan's upper peninsula. Adult worms have also been found in New York (Dougherty 1945), Saskatchewan (Gray *et al.* 1985), Georgia and Lousiana (Prestwood and Pursglove 1974), and South Carolina (Anderson and Prestwood 1981). It appears that *V. alpenae* is not as common as other related protostrongylid nematodes in the southeastern United States because only three deer of nearly 400 searched from 13 southern states were found infected with adult worms (Prestwood and Pursglove 1974). However, Gray *et al.* (1985) reported a prevalence of 19% in WTD of eastern Saskatchewan. They identified *V. alpenae* by experimentally infecting deer with larvae originating from WTD feces collected in central and southeastern Saskatchewan.

First-stage, dorsal-spined larvae of *V. alpenae* are often found at low numbers in deer feces which may be characteristic for this lungworm (Gray *et al.* 1985). If so, this could be a selective disadvantage for *V. alpenae* in areas where *P. tenuis* is also present. *P. tenuis* probably outcompetes the less numerous lungworm, especially if cross-immunity exists. This could explain the higher prevalence of *V. alpenae* in Saskatchewan where prevalence of *P. tenuis* in WTD is only 0.2% (Wasel 1995).

Anderson (1963) surveyed WTD from Algonquin Provincial Park in Ontario for *P. tenuis,* and acknowledged that *V. alpenae* might be present but failed to find any "during numerous detailed examinations of the lungs". Gray *et al.* (1985) determined that larval stages of *V. alpenae* are smaller than other related protostrongylid nematodes. I found evidence that *V. alpenae* might be present in WTD of the upper peninsula, in that smaller L1s were seen in feces.

The geographic distribution of *P. tenuis*, *P. andersoni*, and *V. alpenae* appear to overlap, however, *P. tenuis* is probably the most prevalent and widespread of the three in WTD of eastern North America. This seems feasible because more adult *P. tenuis* have been found despite efforts to locate the others, coupled with the fact that cross-immunity between these closely related parasites probably exists. Experimental studies using unidentified dorsal-spined larvae (*i.e.*, larvae found in feces of deer without successfully locating adult *P. tenuis*) would clarify ranges of closely related parasites and might answer questions regarding cross-immunity between protostrongylid nematodes.

In summary, prevalence of *P. tenuis* in WTD is most accurately assessed by locating adult worms in heads because it is specific for identifying meningeal worm. Results from this study were consistent with other studies around the Great Lakes region (Table 2-5).

Larvae of *P. tenuis* in feces of WTD reach peak numbers by early spring, often when deer leave wintering-areas, thus spreading large numbers of larvae over great distances. However, during this study deer remained in wintering-areas later than usual because of harsh weather which increased the potential to create focal areas of infected gastropods.

The significance of deer yards as potential foci for transmission in the upper peninsula, however, appears limited. Concentrated distributions of L1s in the environment probably create scattered pockets of infected gastropods that may be overlooked by passing ungulates. This could be advantageous for moose if they avoid these areas. Winter logging practices may alter spatial distributions of potential foci by luring deer into areas they would not select naturally. This could be harmful for moose if winter concentrations of WTD are lured into areas where moose inhabit and terrestrial gastropods are present in spring and summer.

Table 2-1. Prevalence and intensity of adult *Parelaphostrongylus tenuis* in white-tailed deer of Michigan's upper peninsula by county in 1995.

County	Number Infected	Prevalence (%)	Mean Intensity
Alger	3 (5)*	60	2.0 (1.0)**
Baraga++	15 (33)	46	1.5 (0.6)
Delta	13 (20)	65	1.8 (1.1)
Dickinson	1 (2)	50	1.0 (0)
Houghton	1 (3)	33	1.0 (0)
Iron++	6 (19)	32	1.2 (0.4)
Marquette++	2 (7)	29	1.0 (0)
Menomonie	12 (19)	63	2.5 (1.4)
Ontonogan	4 (9)	44	2.0 (1.4)
Unknown	12 (41)	29	1.7 (1.0)
Total	69 (158)	44	1.7 (1.1)

*(Number Examined)
**(± 1 Standard Deviation)
++ Counties that encompass the primary range of translocated moose and offspring

Table 2-2. Prevalence and intensity of adult *Parelaphostrongylus tenuis* in white-tailed deer by age class in 1995.

Age Class	Number Infected	% Infected	Mean Intensity
Fawn	14 (51)*	28	1.0 (0)**
Yearling	22 (42)	52	2.0 (1.4)
Adult	33 (65)	51	1.9 (0.9)
Total	69 (158)	44	1.7 (1.1)

*(Number examined)
**(± 1 Standard deviation)

Table 2-3. Prevalence of spine-tailed, first-stage larvae of *Parelaphostrongylus tenuis*, or close relatives, in deer feces by season.

	Number of Fecal Samples Examined	Number Infected	% Prevalence
Summer 1995	61	38	62
Autumn 1995	34	24	71
Winter 1995-96	81	45	56
Spring 1996	42	30	71
Total	218	137	63

Table 2-4. Summary information and results from white-tailed deer examined for adult muscleworm, *Parelaphostrongylus andersoni*.

Date Collected	Sex	Age Class	Cause of Death	Larvae in Pellets	*P. tenuis* in head	Muscle Examined	P. andersoni
03/96	male	yearling	winter kill	0	0	backstrap	0
03/96	female	adult	winter kill	0	0	backstrap and hindquarter	0
04/96	male	yearling	road kill	0	--	backstrap	0
04/96	female	adult	winter kill	0	0	backstrap	0
02/97	female	adult	road kill	+	--	backstrap	0

-- not examined
0 none found
+ larvae found

Table 2-5. Prevalence of adult *Parelaphostrongylus tenuis* found in white-tailed deer from areas in the Midwest.

Location	Number Infected / Number Examined (% Prevalence)	Reference
Michigan	36 / 79 (46)	DeGuisti 1955
	436 / 836 (57)	DeGuisti 1963
	69 / 158 (44)	This study
Minnesota	17 / 51 (33)	Loken *et al.* 1965
	69 / 140 (49)	Karns 1967
	311 / 379 (82)	Slomke *et al.* 1995
Ontario	10 / 30 (33)	Anderson 1956
	71 / 172 (41)	Anderson 1963
Southeastern Manitoba	92 / 169 (54)	Wasel 1995
Wisconsin	13 / 34 (38)	Samuel and Trainer 1969
	45 / 78 (58)	Dew 1988
	37 / 98 (38)	Boppel 1993 Unpublished

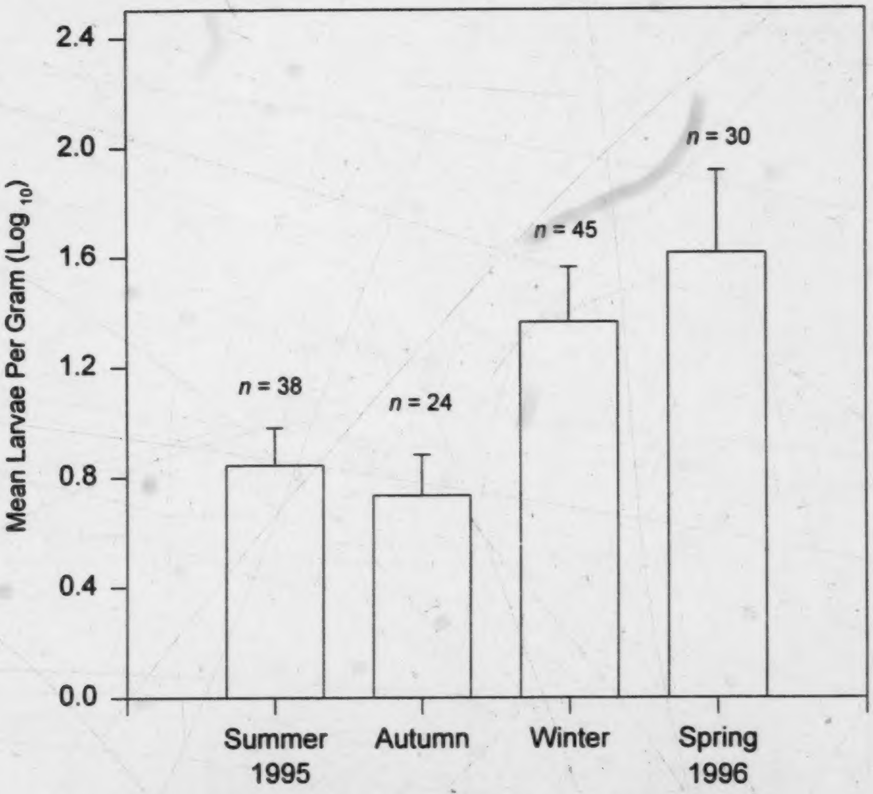


Figure 2-1. Number of first-stage, dorsal-spined nematode larvae in feces of deer by season, 1995-1996. One outlier for Spring 1996 was omitted. Bars represent one standard error.

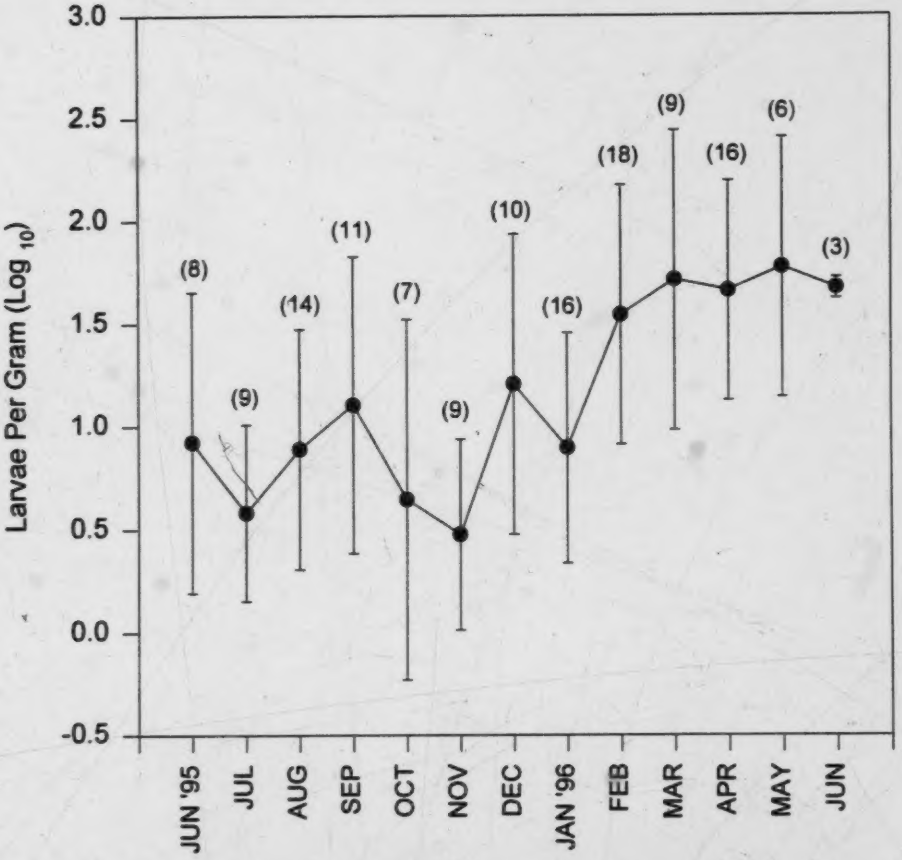


Figure 2-2. Numbers of first-stage, dorsal-spined nematode larvae in feces of deer, 1995 - 1996. Number of fecal groups examined in parentheses, omitting one outlier for May 1996. Bars represent one standard error.

Literature Cited

Anderson, R.C. 1956. *Elaphostrongylus odocoilei* Hobmaier and Hobmaier, 1934 in the cranial case of *Odocoileus virginianus borealis* Miller. Canadian Journal of Zoology 34: 167-173.

-------- 1963. The incidence, development, and experimental transmission of *Pneumostrongylus tenuis* Dougherty (Metastrongyloidea: Protostrongylidae) of the meninges of white-tailed deer (*Odocoileus virginianus borealis*) in Ontario. Canadian Journal of Zoology 41: 775-792.

-------- 1972. The ecological relationships of meningeal worm and native cervids in North America. Journal of Wildlife Diseases 8: 304-310.

Anderson, R.C. and A.K. Prestwood. 1981. Lungworms. Pages 266-317 *In* Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.), Diseases and parasites of white-tailed deer. Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida. 458 pp.

Baker, H.B. 1958. Land snail dispersal. The Nautilus 71: 141-147.

Behrend, D.F. 1970. The nematode, *Pneumostrongylus tenuis*, in white-tailed deer in the Adirondacks. New York Fish and Game Journal 17: 45-49.

-------- and J.F. Witter. 1968. *Pneumostrongylus tenuis*, in white-tailed deer in Maine. The Journal of Wildlife Management 32: 963-966.

Bindernagel, J.A. and R.C. Anderson. 1972. Distribution of meningeal worm in white-tailed deer in Canada. The Journal of Wildlife Management 36: 1349-1353.

Bogaczyk, B.A. 1992. A search for Parelaphostrongylus andersoni in white-tailed deer from Maine. Journal of Wildlife Diseases 28: 311-312.

Bogaczyk, B.A., W.B. Krohn, and H.C. Gibbs. 1993. Factors affecting *Parelaphostrongylus tenuis* in white-tailed deer (*Odocoileus virginianus*) from Maine. Journal of Wildlife Diseases 29: 266-272.

Boppel, P. J. 1993. Prevalence of adult *Parelaphostrongylus tenuis* in white-tailed deer (*Odocoileus virginianus*) of Wisconsin in an area proposed for reintroduction of elk. Unpublished report, University of Wisconsin, Stevens Point. 14 pp.

Boycott, A.E. 1934. The habitats of land mollusca in Britain. Journal of Ecology 22: 1-38.

Carpenter, J.W., H.E. Jordan, and B.C. Ward. 1973. Neurologic disease in wapiti naturally infected with meningeal worms. Journal of Wildlife Diseases 9: 148-153.

Clarke, A.H., J.P. Kelsall, and G.R. Parker. 1968. The land snail fauna of Fundy National Park, New Brunswick. National Museum of Canada: Contributions to Zoology, Bulletin IV 223: 5-22.

DeGuisti, D.L. 1955. The occurrence of a protostrongylid nematode in the meninges of Michigan deer. The Journal of Parasitology 41(2):42 (abstract).

-------- 1963. Incidence and distribution of *Elaphostrongylus odocoilei* in Michigan deer herd. Journal of Parasitology 49(Suppl.): 47.

Dew, T.L. 1988. Prevalence of Parelaphostrongylus tenuis in a sample of hunter-harvested white-tailed deer from a tri-county area in northeastern Wisconsin. Journal of Wildlife Diseases 24: 720-721.

Dikmans, G. 1934. Lungworms collected from deer, *Odocoileus virginianus*, in Michigan. Proceedings of the Helminthological Society of Washington, Vol. 2(1): 59 (abstract).

Dougherty, E.C. 1945. The nematode lungworms of North American deer. Parasitology 36:199-208.

Edwards, W.H. 1995. *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae) in white-tailed deer (*Odocoileus virginianus*) of northeastern Wyoming. M.Sc. Thesis Report. University of Wyoming, Laramie. 83 pp.

Garner, D.L. and W.F. Porter. 1991. Prevalence of *Parelaphostrongylus tenuis* in white-tailed deer in northern New York. Journal of Wildlife Diseases 27: 594-598.

Gilbert, F.F. 1973. *Parelaphostrongylus tenuis* (Dougherty) in Maine: 1 - The parasite in white-tailed deer (*Odocoileus virginianus*, Zimmerman). Journal of Wildlife Diseases 9: 136-143.

Gleich, J.G. and F.F. Gilbert. 1976. A survey of terrestrial gastropods from central Maine. Canadian Journal of Zoology 54: 620-627.

Gray, J.B., W.M. Samuel, A.W. Shostak, and M.J. Pybus. 1985. *Varestrongylus alpenae* (Nematoda: Metastrongyloidea) in white-tailed deer (*Odocoileus virginianus*) of Saskatchewan. Canadian Journal of Zoology 63: 1449-1454.

Karns, P.D. 1967. *Parelaphostrongylus tenuis* in deer in Minnesota and implications for moose. The Journal of Wildlife Management 31: 299-303.

Kearney, S.R. and F.F. Gilbert. 1976. Habitat use by white-tailed deer and moose on sympatric range. The Journal of Wildlife Management 40: 645-657.

Kralka, R.A. 1986. Population characteristics of terrestrial gastropods in boreal forest habitats. The American Midland Naturalist 115: 156-164.

Lankester, M.W. 1987. Pests, parasites and diseases of moose (*Alces alces*) in North America. Swedish Wildlife Research Viltrevy, Supplement 1, Part 2: 461-489.

Lankester, M.W. and P.L. Hauta. 1989. *Parelaphostrongylus andersoni* (Nematoda: Elaphostrongylinae) in caribou (*Rangifer tarandus*) of northern and central Canada. Canadian Journal of Zoology 67: 1966-1975.

Mason, P.C. 1989. *Elaphostrongylus cervi* - a review. Surveillance 16: 3-10.

Michigan Department of Natural Resources (MDNR). 1996. 1938-1996 Michigan deer population figures. Unpublished. 1 pp.

Ozoga, J.J. and L.W. Gysel. 1972. Response of white-tailed deer to winter weather. The Journal of Wildlife Management 36: 892-896.

Peterson, W.J. and M.W. Lankester. 1991. Aspects of the epizootiology of *Parelaphostrongylus tenuis* in a white-tailed deer population. Alces 27: 183-192.

Peterson, W.J., M.W. Lankester, and M.R. Riggs. 1996. Seasonal and annual changes in shedding of *Parelaphostrongylus tenuis* larvae by white-tailed deer in northeastern Minnesota. Alces 32: 61-73.

Prestwood, A.K. 1972. *Parelaphostrongylus andersoni* sp. n. (Metastrongyloidea: Protostrongyloidea) from the musculature of white-tailed deer (*Odocoileus virginianus*). The Journal of Parasitology 58: 897-902.

Prestwood, A.K. and S.R. Pursglove. 1974. *Leptostrongylus alpenae* in white-tailed deer (*Odocoileus virginianus*) of Georgia and Louisiana. The Journal of Parasitology 60: 573.

Prestwood, A.K., V.F. Nettles, and F.E. Kellogg. 1974. Distribution of muscle worm, (*Parelaphostrongylus andersoni*), among white-tailed deer of the southeastern United States. Journal of Wildlife Diseases 10: 404-409.

Prestwood, A.K., and J.F. Smith. 1969. Distribution of meningeal worm (*Pneumostrongylus tenuis*) in deer in the southeastern United States. The Journal of Parasitology 55: 720-725.

Prestwood, A.K., V.F. Nettles, and F.E. Kellogg. 1974. Distribution of muscle worm, (*Parelaphostrongylus andersoni*), among white-tailed deer of the southeastern United States. Journal of Wildlife Diseases 10: 404-409.

Pursglove, S.R. 1977. Helminth parasites of white-tailed deer (*Odocoileus virginianus*) from New Jersey and Oklahoma. Proceedings of the Helminthological Society of Washington 44: 107-108.

Pybus, M.J., and W.M. Samuel. 1981. Nematode muscleworm from white-tailed deer of southeastern British Columbia. The Journal of Wildlife Management 45: 537-542.

-------- and --------. 1984. *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae) and *P. odocoilei* in two cervid definitive hosts. The Journal of Parasitology 70: 507-515.

Pybus, M.J., W.M. Samuel, D.A. Welch, and C.J. Wilke. 1990. *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae) in white-tailed deer in Michigan. Journal of Wildlife Diseases 26: 535-537.

Renecker, L.A. and R.J. Hudson. 1986. Seasonal foraging rates of free-ranging moose. The Journal of Wildlife Management 50: 143-147.

Rogers, L.L. 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. The Journal of Wildlife Management 51: 330-333.

Samuel, W.M. and R.L. Beaudoin. 1966. Evaluation of two survey methods for detection of helminth infections in white-tailed deer (Odocoileus virginianus). Bulletin of th Wildlife Disease Association 2: 100-107.

Samuel, W.M. and J. B. Gray. 1982. Evaluation of the Baermann technique for recovery of lungworm (Nematoda: Protostrongylidae) larvae from wild ruminants. Biennial Symposium Wild Sheep and Goat Council 3: 232-243.

Samuel, W.M. and D.O. Trainer. 1969. A technique for survey of some helminth and protozoan infections of white-tailed deer. The Journal of Wildlife Management 33: 888-894.

Samuel, W.M., T.R. Platt, and S.M. Knispel-Krause. 1985. Gastropod intermediate hosts and transmission of *Parelaphostrongylus odocoilei*, a muscle-inhabiting nematode of mule deer, *Odocoileus h. hemionus*, in Jasper National Park, Alberta. Canadian Journal of Zoology 63: 928-932.

Saunders, B.P. 1973. Meningeal worm in white-tailed deer in northwestern Ontario and moose population densities. The Journal of Wildlife Management 37: 327-330.

Schmitt, S.M., H.R. Hill, and T.M. Cooley. 1989. Upper Peninsula brainworm incidence survey - 1989. Michigan Department of Natural Resources, Wildlife Division Report Number 3109. 8 pp.

Severinghaus, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. The Journal of Wildlife Management 13: 195-216.

Shostak, A.W., and W.M. Samuel. 1984. Moisture and temperature effects on survival and infectivity of first-stage larvae of *Parelaphostrongylus Odocoilei* and *P. tenuis* (Nematoda: Metastrongyloidea). The Journal of Parasitology 70: 262-269.

Skinner, W.R. and E.S. Telfer. 1974. Spring, summer, and fall foods of deer in New Brunswick. The Journal of Wildlife Management 38: 210-214.

Slomke, A.M., W.M. Lankester, and W.J. Peterson. 1995. Infrapopulation dynamics of *Parelaphosrongylus tenuis* in white-tailed deer. Journal of Wildlife Disease 31: 125-135.

Smith, H.J., R.M. Archibald, and A.H. Comer. 1964. Elaphostrongylosis in maritime moose and deer. Canadian Veterinary Journal 5: 287-296.

Thomas, J.E. and D.G. Dodds. 1988. Brainworm, *Parelaphostrongylus tenuis*, in moose, *Alces alces*, and white-tailed deer, *Odocoileus virginianus*, of Nova Scotia. The Canadian Field-Naturalist 102: 639-642.

Uhazy, L.S., J.C. Holmes, and J.G. Stelfox. 1973. Lungworms in th rocky mountain bighorn sheep of western Canada. Canadian Journal of Zoology 51: 817-824.

Van Deelen, T.R., K.S. Pregitzer, and J.B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. The American Midland Naturalist 135: 181-194.

Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan. Journal of Forestry 63: 523-529.

Wasel, S.M. 1995. Meningeal worm, *Parelaphostrongylus tenuis* (Nematoda), in Manitoba, Saskatchewan, and North Dakota: Distribution and ecological correlates. Department of Zoology, University of Alberta, Edmonton. 100 pp.

Whitlaw, H.A., and M.W. Lankester. 1994. A retrospectiv[illegible]valuation of the effects of parelaphostrongylosis on moose. Canadian Journal of Zoology 72: 1-7.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey. 718 pp.

Personal Communications

David R. Anderson. 1993. Pennsylvania State University, Professor of Biology, Fayette, Pennsylvania. Mailed unpublished data to Dr. William Samuel at University of Alberta, Edmonton, with permission to use.

CHAPTER III. ECOLOGY OF GASTROPODS IN MICHIGAN'S UPPER PENINSULA IN RELATION TO TRANSMISSION OF *PARELAPHOSTRONGYLUS TENUIS*

Introduction

Meningeal worm, *Parelaphostrongylus tenuis*, is a common parasite of the central nervous system in WTD of eastern North America (Anderson and Prestwood 1981). Infected WTD show few clinical signs but *P. tenuis* often causes fatal neurological disease in moose. Therefore, anywhere infected WTD and moose are sympatric there is reason for concern, particularly where moose numbers are few.

Moose were reintroduced into Michigan's upper peninsula in 1985 and 1987. Since then, 17 of 53 diagnosed deaths (32%) in moose have been attributed to *P. tenuis*-induced neurological disease (MDNR 1997). Although the role of *P. tenuis* is not clearly understood, numbers of moose are much lower than predicted despite apparently stable reproductive rates of radio-collared females (Aho 1995, MDNR 1996).

Meningeal worm has a two-host life cycle with white-tailed deer serving as definitive host and a variety of terrestrial snails and slugs as intermediate hosts. Gastropods become infected by crawling on or near deer feces infected with first-stage larvae (L1s), or by encountering larvae in soil contaminated by infected feces. Larvae develop within the gastropods to a third-stage that is infective to WTD and moose. Ungulate hosts acquire *P. tenuis* by accidentally ingesting infected gastropods while feeding.

Many different species of snails and slugs have been identified as suitable intermediate hosts for *P. tenuis* (see Table 1-1). The ecology of some important intermediate host species has been studied in Ontario (Lankester and Anderson 1968), New Brunswick (Upshall *et al.* 1986), Pennsylvania (Maze and Johnstone 1986), and Indiana (Platt 1989). But ecology of gastropods related to the transmission of *P. tenuis* has never been studied in the upper peninsula. Determining abundance, distribution and prevalence of infection in gastropods should provide insight to the potential risks for moose in Michigan's upper peninsula to acquire meningeal worm.

Prevalence of *P. tenuis* infection within terrestrial gastropods is usually very low (<1%) (Gleich *et al.* 1977, Kearney and Gilbert 1978, Pitt and Jordan 1995). However, gastropods should have a greater chance of becoming infected if they are in areas that are highly contaminated with deer feces. Deer in the upper peninsula congregate in areas known as "yards" usually in conifer lowlands and recently logged areas during winter to avoid deep snow and facilitate feeding (Bartlett 1950, Verme 1965, Van Deelen *et al.* 1996). They are also found in large numbers on private lands where people provide food. These areas are highly contaminated with deer feces and if terrestrial gastropods are present, potentially serve as foci of infected gastropods.

For transmission to ungulates, focal areas of infected gastropods must also be inhabited by definitive hosts during snow-free periods when gastropods are available to be eaten. Lankester and Anderson (1968) suggest that on Navy Island, Ontario, low, damp, forested habitat, where deer dispersed during the day and where infected gastropods were most common, could serve as foci for transmission. Maze and Johnstone (1986) reported that a reclaimed strip mine often used by deer, with dense ground cover suitable for gastropods, yielded 81% of the gastropods collected in their study and 92% of the infected gastropods. Kearney and Gilbert (1978) suggested that habitat with white birch (*Betula paperifera*) as a constituent species, had high potential for *P. tenuis* transmission, because such habitats were used heavily by both moose and deer and because gastropods were abundant there. Upshall *et al.* (1986) supported this idea and, along with Raskevitz *et al.* (1991), suggested that for similar reasons hardwood dominated habitat had best potential for transmission.

Robb and Samuel (1990) suggested seasonal foci for transmission of lungworms to bighorn sheep (*i.e.*, aspen stands in autumn and grassy openings during spring), because of seasonal use by bighorns and availability of infected gastropods. More recently, Lankester and Peterson (1996) suggested greater prevalence of infected gastropods in a traditional deer wintering area than on summer range. Unfortunately, conclusions were based on only 10 infected gastropods of 12,096 examined. They suggested that importance of such foci for transmission to definitive hosts was limited.

Rationale

At the time this study was initiated, moose appeared to be increasing in numbers in the upper peninsula despite the abundance of WTD and presence of *P. tenuis*. It was unclear if foci exist or how these areas may influence transmission of *P. tenuis* to moose, so the objectives of my study were to 1) determine species abundance and distribution of terrestrial gastropods and identify broad habitat types that appear more suitable for gastropods, 2) determine which species were most often infected with *P. tenuis* larvae, and 3) examine the idea of foci of transmission (*i.e.*, determine if infected gastropods occur at high densities in areas/habitats frequented by deer or moose). The following hypotheses were tested:

H1o: Densities of gastropods will be random across varying habitats and disturbed areas, **H1a**: Densities of gastropods will vary greatly according to habitat and human disturbance.

Based on published information about the ecology of terrestrial gastropods, I predicted that gastropods would be more abundant in particular habitats because of various environmental factors.

H2o: Many species of gastropods will be infected naturally with *P. tenuis*, **H2a**: Few species of gastropods will be infected naturally with *P. tenuis* larvae.

Based on results of published surveys of gastropods for *P. tenuis*, I predicted that few species of gastropods would be infected with *P. tenuis* and that those infected would probably be the most widely-distributed species.

H3o: Infected gastropods will be randomly distributed throughout areas inhabited by deer or moose. **H3a**: Densities of infected gastropods will vary between areas inhabited by deer or moose.

Based on limited published information on *P. tenuis* and related parasites, and the fact that definitive host WTD congregate in wintering areas on an annual basis, I predicted that concentrations of infected gastropods most likely exist.

Methods

Selection of Gastropod Collection Sites

In 1995, 22 sites in Baraga County were selected for collection of gastropods (Figure 3-1). Areas were selected according to four broad habitat types which were:

1) mixed conifer/deciduous (*n* = 7),
2) predominately conifer (*n* = 4),
3) predominately deciduous (*n* = 8), and
4) grass (*n* = 3).

Classification was based on the number and ratio of trees (conifer to deciduous) along 100 m transects where gastropods were collected.

Sites were also selected according to 'definitive host-use categories' which were:

1) areas where deer concentrated during winter 1994 and summer 1995 ($n = 8$),
2) areas where moose were known to inhabit ($n = 4$), and
3) areas with few deer and no signs of moose, hereafter termed 'miscellaneous' ($n = 10$).

Areas where deer concentrated had signs of deer such as deer trails, fecal pellets, or visible concentrations of deer. Areas where moose were known to inhabit were located according to geographical bearings acquired by Michigan Department of Natural Resources (MDNR) from radio telemetry, and confirmed by presence of tracks and/or signs of browsing. Miscellaneous areas were sites originally selected by habitat type and had no major concentrations of WTD and no signs of moose.

In 1996, 13 areas in Baraga County were selected for gastropod collection (Figure 3-1). These were:

1) five areas, called "yards", where deer concentrated during winter of 1995-96,
2) four areas where moose had been located the previous summer and/or current spring, and
3) four repeat-collection areas from 1995 which included one deer yard.

The four repeat collection sites were compared to 1995 results for the same time period as 1996 to see if gastropod composition had changed following the harsh winter of 1995-96.

Sites were selected according to use by deer or moose in 1996, so vegetative descriptions were completed secondarily. Broad habitat categories were:

1) mixed conifer-deciduous sites ($n = 4$),
2) predominantly conifer sites ($n = 4$),
3) predominantly deciduous sites ($n = 3$), and
4) grass ($n = 2$).

Habitat Description

Habitat surveys were completed 10 - 21 August 1995 and 1996. Data were gathered at 20 m intervals where gastropods were collected along 100 m transects. Data recorded at each interval were: 1) number and identification of trees in a 4 m circle including diameter at breast height (dbh) for trees >2 cm dbh, 2) number and identification of plant species on the ground in a 1 m^2 area, 3) depth (cm) of soil (AH layer) and averaged for the site, and 3) percent canopy cover averaged for the site and rounded to the nearest 10%. Canopy cover was determined using a home-made apparatus which consisted of a cardboard tube and aluminum foil covering one end with a pin-hole in the center. Looking into the open end, "light" or "dark "was observed through the pin hole at the opposite end. Five observations were recorded at each interval and percent "dark" observations were averaged for the site.

Subcanopy trees were counted and included with tree data. Subcanopy shrubs were counted at ground level and included with ground vegetation data. Plant species were identified using various field guides (Voss 1972, Newcomb 1977, Barnes and Wagner 1981, Voss 1985). Some plant species were confirmed by Dr. Robert Freckman at the University of Wisconsin, Stevens Point. Vegetation surveys were limited to immediate areas where gastropods were collected to represent communities inhabited by the gastropods.

Additional soil characteristics such as soil type, permeability, and approximate depth of the water table were obtained from soil surveys for Baraga County conducted by the Soil Conservation Service of the United States Department of Agriculture (Berndt 1988). For summarized descriptions of collection sites for 1995 and 1996, see Appendix Ia-c and Appendix IIa-c, respectively.

Collection and Identification of Gastropods

Gastropods were collected at 20 m intervals along 100 m permanent plot transects, one transect per site. To attract gastropods, corrugated cardboard (1 m^2) was placed at each interval (Boag 1982, 1990). In 1995, collections were done weekly from 05 June to 30 August and biweekly from 1 September to 11 October. In 1996, collections were done weekly 10 June to 12 August. Cardboards were moistened on the evening prior to collection to attract gastropods and covered with plastic sheeting to slow evaporation. Cardboards were examined between 0600 and 1100 hrs, or between 0800 and 1300 hrs during periods of rainfall, when they were still moist. Gastropods were taken from both sides and the inner layer of the cardboard, and both sides of the plastic sheets. Cardboards were replaced when they became too ragged to manipulate or if destroyed by animals. Replacement cardboards were placed on the same spot or directly adjacent if a large amount of mold was present. Cardboards placed in repeat collection sites for 1996 were staggered, approximately 10 m, between previous carboard placements of 1995.

Snails and slugs were placed in plastic compartmental boxes, lined on the inside cover with moist cheese-cloth to avoid desiccation, and stored on ice in a plastic cooler for transport. Gastropods were stored separately by collection area at approximately 9°C for

24-48 hrs and sorted by species prior to the digestion process. Identifications were made using keys by Burch (1962), Burch and Jung (1988), and Burch and Pierce (1990). Identifications of gastropods were verified by Dr. John Burch, The University of Michigan, Ann Arbor.

Once identified, gastropods were placed in small 5 ml test tubes, one to four per tube of the same species and collection area. Slugs and larger species of snails were minced with a scalpel or fine scissors before placing them in 50 ml tubes. Date of collection, date of examination, collection site, species, number of animals per tube, and a reference number were recorded. Three to 4.5 ml of artificial digesting solution (0.7 ml concentrated HCl and 0.6 gm pepsin powder per 100 ml distilled water (Samuel *et al.* 1985)) were added to each 5 ml test tube, while 6 to 8 ml were added to the 50 ml tubes. Gastropods were crushed with wooden sticks and the solutions stirred vigorously. During preliminary trials, different sizes of gastropods were incubated for varying periods of time at 38 - 40 C. Eight hrs was the optimal incubation time for all gastropods except the very large snail, *Triodopsis albolabris* which incubated 16 hrs. All tubes were agitated at least once during incubation to assist breakdown of the tissue.

Following incubation each tube of solution was examined individually, rinsing the liquid into small 6 cm plastic petri dishes and viewed at 25X using a dissecting microscope. Dishes remained untouched for approximately 3 min which allowed larvae to settle to the bottom of the dish. The dishes had small grids etched in the bottom to assist in orientation.

Large numbers of gastropods were collected which occasionally required pooling of individuals prior to digestion. Previous studies have handled the problem of multiple larvae by assuming that all larvae came from one snail (Whitlaw *et al.* 1996). Although this is a reasonable assumption in cases of low overall prevalence, it is not a certainty. Therefore, I excluded data from test tubes with multiple gastropods and multiple larvae for calculations of prevalence and intensity. Thus, results describing prevalence and intensity of larvae in gastropods show slightly lower totals of gastropods than results on abundance.

Two species of slugs, *Arion fasciatus* and *Arion subfuscus,* were collected (511 total) during June of 1995. Slugs of this genus have a thick coating of slime and exceptionally firm tissue of the foot so they are probably poor intermediate hosts of *P. tenuis.* Despite the fact that these introduced slugs are fairly common throughout northeastern North America (Getz and Chichester 1971), only one individual of the species *Arion circumscriptus* has been found to be infected with *P. tenuis* (Lankester and Anderson 1968). In addition to their low potential for infection, it took many hours to digest these slugs artificially. Of the 511 *A. fasciatus* and *A. subfuscus* collected in June 1995 and examined for *P. tenuis*, none were infected. For these reasons, the genus *Arion* were not collected after June 1995 and they are not included in any analyses or results.

Two species of snails, *Discus cronkhitei* and *Discus catskillensis*, look nearly identical except for subtle differences in the shape of the shell (Burch 1962). Both species were abundant and often found together. After some initial sampling, I did not separate them by species. I acknowledge that both shell shapes were present but consider them collectively as *Discus* spp. throughout this report.

Processing and Identification of Larvae

Larvae were collected, a majority alive and moving, using a 1 cc syringe and large gauge needle with the beveled tip removed. They were placed in 4 ml vials with approximately 3 ml of 10% glycerin-alcohol that was heated to near-boiling in a microwave oven immediately prior to addition of larvae. This technique caused serious problems wherein some larvae coiled tightly and eosophagus' buckled.

Normally, third-stage larvae of *P. tenuis* are large (minimum about 900 μm), relatively translucent and die in a characteristic "c" shape (Anderson 1963). Large larvae that fit the classic description (Anderson 1963), were assumed to be those of *P. tenuis*. However, some larvae were smaller and granular in appearance because they were killed in alcohol heated by microwave. Therefore, drawings were made from a random subsample of larvae (97 total) with the aid of a compound microscope, in direct light and/or phase contrast settings, with a camera lucida attachment. Measurements of total length and distinguishing characteristics were taken from the drawings using a Summa Sketch Plus digitizing tablet. For smaller larvae (700 - 799 μm), locations of the various body parts were measured as percent of the total body length. Larvae were considered *P. tenuis* if they fit the classic descriptions or had at least four of the five following characteristics: 1) shape of the buccal capsule, 2) correct location of the nerve ring 3) correct location of the excretory pore, 4) correct location of the terminal end of the eosaphagus, and 5) presence of a constriction or spine at the tip of the tail. Larvae that were ≤ 699 μm or too tightly coiled to see defining characteristics were excluded from the data set.

Measurements from the subset of larvae were comfirmed by comparing them to measurements of *P. tenuis* made by Anderson (1963) and Ballantyne and Samuel (1984). In addition, all specimens were compared to confirmed *P. tenuis* L3s that were reared in laboratory-raised (*Triodopsis* spp.) snails at University of Alberta and more from Lakehead University. Laboratory-raised snails and larvae were processed using the same techniques for snails and larvae collected from the field sites.

Platt (1978) and Samuel *et al.* (1985) killed and preserved L3s of *P. odocoilei* in hot glycerin-alcohol. It is possible to kill and properly to preserve larvae simultaneously but using a microwave oven to heat the alcohol solution was ineffective. Potential *P. tenuis* larvae were excluded because of difficulty identifying crucial characteristics, therefore, numbers of larvae in gastropods are conservative estimates.

Statistical Methods

Analyses of gastropod data were conducted separately between years because the site selection criteria differed between 1995 and 1996, and the collection season for 1995 was 6 weeks longer than for 1996. All data for both years were analyzed for normal distributions using the Kolmogorov-Smirnov test, and for constant variance using Levine's test or Spearman rank correlation (Zar 1984). If data failed either test, they were transformed, retested for normality and constant variance, and parametric tests were used accordingly (*i.e.*, if power of the analyses were at least 0.80 at $P = 0.05$ level). One-way analyses of variance (1 - way ANOVA) or a t-tests were calculated. Differences between multiple categories were determined using Tukey's Honestly-Significant-Difference multiple comparison test (Zar 1984).

If transformed data did not pass normality or variance tests, original non-transformed data were analyzed using non-parametric statistics. Kruskal-Wallis 1-way ANOVA or Mann-Whitney-U statistics were used. Differences between multiple groups were determined using Dunn's multiple comparison test (Zar 1984). Statistics were done using the Statistical Package for the Social Sciences (SPSS) computer software and results were considered significant at $P \leq 0.05$.

To see what components of habitat best explain the distribution of gastropods between collection sites, canonical correspondence analysis (CCA) was done using Canonical Community Ordination (CANOCO) computer software (ter Braak 1987a), for both 1995 and 1996. This technique is useful because it offers visual ordination diagrams that express spatial patterns of floristic, and in this case, gastropod composition. A descriptive and exploratory technique, CCA is often used to summarize community data by correlating environmental gradients with species abundances (Kent and Coker 1995). More specifically, ordinations determine the order of variance in species abundance data explained by linear combinations of environmental variables (ter Braak 1987b). Percent canopy cover (CC), depth of top soil (SD), soil type (ST), permeability of soil (PM) and depth of water table (WT) were five environmental variables used in the analyses. Environmental variables are shown as arrows on the ordination diagrams, the angle of the arrows from the axis represents the correlation of each variable with the axis. Biplot diagrams show the relationship between the species and environmental variables; that is, the closer a species (noted as abbreviations of scientific names) is to the head of the arrow, the more positively correlated the species is to the environmental variable (ter Braak 1987b).

Abundance of plant species and abundance of gastropod species per site were analyzed simultaneously to show relationships between vegetation and numbers of gastropods in response to the five environmental variables. Species abundance data were modified by natural log transformation to correct for large numbers of zeroes in the data set (ter Braak 1987) and rare species were down-weighted for more accurate correlations. Results were considered significant at $P \leq 0.05$.

For clarity of presentation, not all plant species were included on the diagrams. Widely-distributed species were clustered in the center of the diagrams, therefore many were removed from the diagrams. Some plant species were not sampled in sufficient numbers to represent the full range of their distribution (< 2% of the total plants identified) and were excluded from the diagrams. See Appendix VIIIa-c for the complete list of plant species identified with their corresponding abbreviations.

Results

Species Composition of Gastropods

A total of 9,552 gastropods representing 12 families, 18 genera, and 22 species, was collected in 1995 and 1996; totals were 5,901 and 3,651, respectively (Table 3-1). The most abundant species was *Zonitoides arboreus,* which accounted for 37% of the gastropods collected.

In 1995, numbers of gastropods per site were significantly higher in mixed conifer-deciduous habitat ($H = 10.1$, $P = 0.02$) than in predominantly conifer, predominantly deciduous, or grass habitats (Figure 3-2). Abundance of gastropods did not differ between definitive host-use categories ($H = 0.3$, $P = 0.86$).

In 1996, abundance of gastropods did not differ between habitat types (*H* = 2.5, *P* = 0.47) (Figure 3-2). However, on average there were more gastropods in deer yards (*t* = 3.2, *P* = 0.01) than in moose-inhabited areas (Figure 3-3).

In 1995, there were significantly more species of gastropods in mixed sites (*F* = 6.8, *P* = 0.003) than in predominantly deciduous or grass sites (Figure 3-4). Numbers of species were not different between deer concentration areas, moose-inhabited sites, or miscellaneous sites (*H* = 3.5, *P* = 0.17).

Species richness in 1996 did not differ between habitat types (*H* = 0.7, *P* = 0.76). However, more species of gastropods were collected in deer yards than moose-inhabited areas (*t* = 3.5, *P* = 0.01).

Repeat collection sites had similar numbers of gastropods both years but numbers of species was higher for site 632 in 1996 than in 1995 (Table 3-2).

Species - Habitat Correlations: 1995

The first two axes of the ordination explain 61% of the variation in the species-environment relationship and 19% of variation in the species data (Table 3-3a). Axes three and four explain only 28.4% additional variance of the species-environment relation and so were not included in the ordination diagrams. Interset correlations showed that canopy cover was the most important variable defining the first axis, soil type and permeability defined the second axis (Table 3-3b). Axis one is correlated with percent canopy cover, so sites on the left side of the ordination offered shaded conditions and sites towards the right were more sunny (Figure 3-5a). The soil related environmental variables define a moisture gradient. Therefore, drier sites are located on the lower half (negative side) of axis two because of sandier soil conditions and higher permeability. Sites located on the upper (positive) end of axis two are very moist because of loam or muck soil types that have lower permeability.

Three of the four broad habitat types show as relatively distinct groups in the ordination (Figure 3-5b). Mixed sites were generally lowland areas with deep top soil of loam and moderate permeability. Site 212 was also lowland but it had mucky soil with low permeability and a relatively open canopy. Sites 413 and 415 were upland mixed habitat with sandy soils and closed canopies of approximately 90%. Most of the predominantly deciduous sites had shallow, sandy soils with higher permeability, except for sites 330 and 532 which had deep loamy soils and lower permeability. Grass sites lacked canopy cover, were soils of silt or loam with moderate permeability. The predominantly conifer sites were scattered on the diagram because they were comprised of different conifer species that tolerate a variety of habitat conditions.

Conifer species of balsam fir (*Abies balsamea*) and eastern hemlock (*Tsuga canadensis*) were found most abundantly with red maple (*Acer rubrum*) in sites 225, 321, and 104 (Figure 3-6a). Site 318 was predominantly black spruce (*Picea mariana*) with some white birch (*Betula paperifera)*. Site 109 had greatest abundance of northern white cedar (*Thuja occidentalis*) and yellow birch (*Betula alleghaniensis*) as well as seedlings of balsam fir. All of these afore-mentioned tree communities had deeper loamy soils that included a relatively deep litter layer. A red pine (*Pinus resinosa*) plantation, site 424, had relatively shallow sandy soil and little canopy cover. Red maple and sugar maple (*Acer saccharum*) were common trees found in nearly all sites, although red maple was slightly more abundant in habitats with deeper soil and greater moisture. Sites with large components of sugar maple offered greatest canopy cover but had relatively shallow soil with corresponding shallow litter. Tree species including trembling aspen (*Populus tremuloides*), iron wood (*Ostrya virginiana*), basswood (*Tilia americanus*), and white ash (*Fraxinus americanus*) were abundant in upland deciduous sites with sandier soil types and greater permeability. Sites 432 and 531 included sugar maple, white ash and black cherry (*Prunus serotina*), had numerous seedlings of balsam fir and offered slightly lower canopy cover.

Species composition of ground cover plants in 1995, also showed a moisture gradient from moist lowland mixed sites to drier upland deciduous sites (Figure 3-6b). Various species of clubmoss (*Lycopodium* spp.), goldthread (*Coptis groenlandiea*), bunch berry (*Cornus canadensis*), partridge berry (*Mitchella repens*), interrupted fern (*Osmunda claytoniana*), and blue beadlily (*Clintonia borealis*) were a few of the plants commonly found in the wet areas. Mountain maple (*Acer spicatum*), Canada white violet (*Viola canadense*), false solomon seal (*Smilacina racemosa*), and sarsasparilla (*Aralia nudicaulus*), were some of the species found in the upland deciduous areas. Common roadside plants such as yarrow (*Achillaea millefolium*), orange hawkweed (*Hieracium aurantiacum*), and oxeye daisy (*Chrysanthemum leucanthemum*) were plants found among the grass areas. Grass species included orchard grass (*Dactylis glomerata*), red top (*Agrostis gigantea*), quack grass (*Elytrigia repens*) and timothy grass (*Phleum pratense*) although these species were not quantified or included in the ordination.

The most widely distributed species of gastropods, *Zonitoides arboreus*, *Discus* spp., *Deroceras laeve*, and *Pallifera dorsalis* cluster near the center of the ordination, which represents their common occurrence in most sites (Figure 3-7). *Cionella lubrica, Zonitoides nitidus*, and *Deroceras reticulatum* were closely associated with wet habitats lacking canopy cover. Gastropods, *Anguispira alternata* and *Helicodiscus parallelus,* were found more abundantly in areas with sandier soil conditions, higher permeability, and greater canopy cover of upland deciduous stands that included sugar maple, trembling aspen and ironwood. Gastropods, *Striatura exigua, Euconulus fulvus, Zoogenetes harpa, Striatura ferrea, Strenotrema fraternum,* and *Punctum minitusum,* were associated with sites that had deep moist top soils of predominantly conifer and mixed composition that included trees such as balsam fir, eastern hemlock, and northern white cedar. Of these apparently conifer-related species, *Striatura exigua* was the most abundant and wide-ranging. *Triodopsis albolabris* was found in moist, mixed forest stands.

Species -Habitat Correlations: 1996

The first two axes of the ordination explain 65% of the variation in the species-environment relationship and 35% of variation in the species data (Table 3-4a). Canopy cover was again the most important variable that defined the first axis and soil depth defined the second axis (Table 3-4b). All four soil characteristics were highly correlated (Figure 3-8a).

All sites in 1996 were relatively moist areas and so separating broad habitat types according to the environmental variables, which collectively define a moisture gradient, did not distinguish habitat types into separate groups (Figure 3-8b). General community structures based on floristic composition were relatively similar in 1996 as in 1995, although the communities were not as clearly defined along a gradient. There are representative communities that include eastern hemlock and northern white cedar, as well as deciduous communities of bass wood (*Tilia americana*) and sugar maple (*Acer saccharum*) with corresponding ground vegetation (Figures 3-9a and 3-9b).

Most importantly, gastropod composition showed similar associations with floristic communities (Figure 3-10). Species associated with relatively drier deciduous sites and higher canopy cover were, again, *Anguispira alternata* and *Helicodiscus parallelus*. A group of gastropod species associated with deep soil communities that included eastern hemlock and northern white cedar, were: *Striatura exigua, Euconulus fulvus, Zoogenetes harpa, Striatura ferrea, Strenotrema fraternum,* and *Punctum minitusum. Deroceras reticulatum, Cionella lubrica,* and *Zonitoides nitidus* were found in similar habitats as in 1995.

Distribution of Infected Species of Gastropods

A total 30 of 5,880 (0.5%) gastropods were found to be infected with *P. tenuis* larvae in 1995. Numbers of larvae in gastropods ranged from 1 to 6 and the mean intensity was 1.4 (± 1.0 s.d.). Eight species of gastropods were infected: *Zonitoides arboreus*, *Zonitoides nitidus*, *Deroceras laeve*, *Discus* spp., *Cionella lubrica*, *Pallifera dorsalis*, *Anguispira alternata* and *Triodopsis albolabris* (Table 3-5).

A total 38 of 3,597 (1.1%) gastropods were infected with *P. tenuis* larvae in 1996. Numbers of larvae ranged from 1 to 19 and the mean intensity was 2.9 (± 3.7 s.d.). Seven species of gastropods were infected in 1996. These were the same species found infected in 1995, except for *Cionella lubrica* which was not infected in 1996 (Table 3-5).

In 1995, numbers of infected gastropods did not differ between habitat types ($H = 3.03$, $P = 0.39$). There tended to be more infected gastropods in areas where deer concentrated, than in areas where moose-inhabited or miscellaneous sites ($H = 5.42$, $P = 0.06$) (Figure 3-11).

In 1996, numbers of infected gastropods did not differ between habitat types ($H = 4.3$, $P = 0.23$). There tended to be more infected gastropods in deer-yard areas than in moose-inhabited areas ($T = 13.5$, $P = 0.07$) (Figure 3-11). Repeat sites had similar numbers of infected gastropods both years (Table 3-2).

In 1995 nearly all intermediate host species were more abundant in mixed habitat than the other three habitat types ($H = 7.45$, $P = 0.06$) (Figure 3-12). In 1996, most intermediate host species were found with similar abundances between habitat types ($H = 0.70$, $P = 0.71$). In both years, fewest gastropods were collected from grass habitats.

Identification of Larvae and Trends in Development

A total 248 larvae, 55 in 1995 and 193 in 1996, were identified as *P. tenuis* larvae. A majority of the larvae were collected alive; their movement and general appearance were similar to 'known' *P. tenuis* larvae from laboratory-raised snails. Measurements were also similar to larvae from laboratory-raised snails and many fit within ranges of measurements from previous studies by direct measurements or by percent of total lengths (Table 3-6).

In 1995, total numbers of larvae (L2s and L3s) were similar between the four broad habitat types ($H = 2.36$, $P = 0.50$). However, total numbers of larvae were higher in areas where deer concentrate, but not significantly ($H = 5.23$, $P = 0.07$) (Figure 3-13).

In 1996, total numbers of larvae were not significantly different between habitat types (*H*= 4.09, *P* = 0.25). Numbers of larvae tended to be higher in gastropods collected from deer-yard sites than from sites inhabited by moose, but not significantly (*T* = 1.95, *P* = 0.08) (Figure 3-13).

A total 170 of 248 larvae (69%) were identified as L3s. Second-stage larvae were differentiated from L3s because of a double cuticle that had the spine still visible. Numbers of infective L3s were highest in August for both 1995 (H = 5.42, P = 0.25) and 1996 (*H* = 2.83, *P* = 0.24) although differences were not significant (Table 3-7).

Discussion

Results of this study support the hypothesis that few species of gastropods would be infected with *P. tenuis*. Only 8 of the 22 species collected were infected and no new intermediate host species were identified. As predicted, the most abundant and widely-distributed species were important intermediate hosts, consistent with related studies (Lankester and Anderson 1968, Maze and Johnstone 1986, Upshall *et al.* 1986, Rowley *et al.* 1987, Platt 1989). An index of parasite abundance (mean intensity of infection x prevalence of infection) (Leong *et al.* 1982, Margolis *et al.* 1982) was calculated for all eight infected species. The index was multiplied by the relative abundance of each species to adjust for varying sample sizes between them (Robb 1987) (Table 3-8). According to the index, the four most important hosts for *P. tenuis* in Michigan's upper peninsula are *Discus* spp., *Anguispira alternata*, *Triodopsis albolabris*, and *Zonitoides arboreus*. Two of these species, *Discus* spp. and *Z. arboreus* were found in all habitat types. *Anguispira alternata* had the second highest index and was found abundantly in upland deciduous and upland mixed habitat types. *Triodopsis albolabris* was usually found in small numbers and slightly more common in mixed habitat. It is a large snail and probably one of the longest lived (Walton 1963), therefore, it has an increased chance for infection with *P. tenuis*. Despite its low abundance, *T. albolabris* is a compatible host for *P. tenuis,* because a majority of those collected were infected and with relatively high intensity. Overall, the distribution of these important species indicate that all habitat types have potential for transmission of *P. tenuis*.

Results from this study indicate, however, that lowland areas may be more important for transmission of *P. tenuis* because of greater abundance of gastropods. Greater numbers of gastropods were found in mixed conifer-deciduous habitat, which were mostly moist lowland areas in 1995. Others found lowlands of mixed-forest had abundant gastropods in central Maine (Gleich and Gilbert 1976), central Ontario (Kearney and Gilbert 1978), New

Brunswick (Clarke *et al.* 1968), and in the Great Smoky Mountains of Tennessee and North Carolina (Getz 1974).

All collection sites were moist lowland areas in 1996, that offered relatively stable micro-environments despite variation in vegetation so mixed sites were not preferred over other types. This supports the idea that moisture is an important requirement for gastropod communities, consistent with other studies (Walton 1963, Clarke *et al.* 1968, Getz 1974, Gleich and Gilbert 1976, Boag 1985, Prior 1985). It also explains why species diversity was greater in mixed sites in 1995 but similar between habitat types in 1996 (Figure 3-4). Species diversity at a roadside collection area (site 632) was greater in 1996 than in 1995. However, the 'recent' species for 1996 were in very low numbers (1 to 6) suggesting that they were not well established (see Appendices Vb and VI).

Cionella lubrica, *Zonitoides nitidus*, and *Deroceras reticulatum*, known intermediate hosts of *P. tenuis*, were associated with wet sites; they were found often near standing water. Other studies also report the affinity of *C. lubrica* and *Z. nitidus* for wet areas (Clarke *et al.* 1968, Andersen and Halvorsen 1984). These species were also associated with open canopy, including roadside grass areas that lacked canopy cover altogether. Lee (1952) also noted that *Z. nitidus* was associated with wet, well-lighted areas in southern Michigan. These species could be important species for transmission of *P. tenuis* to moose, because moose are attracted to open, wet areas. *Cionella lubrica*, *Z. nitidus*, and *D. reticulatum* are probably common along edges of marshy wetland areas that moose frequent in summer.

Although moisture probably affects the distribution of many gastropod species (Walton 1963, Clarke *et al.* 1968, Boag 1985, Prior 1985), *Anguispira alternata*, an important intermediate host, was found abundantly in upland stands of predominantly deciduous or mixed composition and '"...seems capable of enduring the driest situations"' (Latchford 1885 as cited by Clarke *et al.* 1968). *Zonitoides arboreus* was also present at these sites in high numbers, suggesting that some intermediate host species do not require very high moisture regimes.

In addition to moisture, soil pH may also affect species distributions (Strandine 1941, Burch 1955, Maze and Johnstone 1986, Hawkins *et al.* unpublished). Burch (1955) collected gastropods from sites with soil pH ranging from 4.8 to 7.7 and found greatest numbers of gastropods in soils with a pH of 6.3 to 6.7. It appears, however, that particular communities of gastropods tolerate more acidic conditions and are often found in habitats with high components of conifer. Hawkins *et al.* (unpublished) found *Zoogenetes harpa*, *Vertigo gouldi*, *Discus cronkhitei*, *Euconulus fulvus*, *Zonitoides arboreus*, and *Columella edentula* were associated with lower pH values (their total range of pH was 3.4 to 5.1) in spruce-dominated communities of northwestern Ontario. I found *Euconulus fulvus*, *Zoogentes harpa*, *Striatura exigua*, *Striatura ferrea*, *Strenotrema fraternum*, and *Punctum minitusum* were relatively abundant in sites with components of balsam fir, eastern hemlock, and/or northern white cedar. Clarke *et al.* (1968) found similar species of gastropods as this study, in conifer stands of Fundy National Park in New Brunswick. Gleich and Gilbert (1976) in Maine also found *E. fulvus*, *Z. harpa*, *S. exigua*, and *S. ferrea*.associated with conifer communities of spruce-fir or northern white cedar. Andersen and Halvorsen (1984) found *Z. harpa* and *E. fulvus* in boreal conifer habitat of arctic Norway, and *E. fulvus* was more wide-ranging of the two. Getz (1974) also found high diversity of snail species in areas with large components of eastern hemlock. Of the conifer-associated species found in this study, *Strenotrema fraternum* is a known intermediate host for *P. tenuis* (Maze and Johnstone 1986), but none were infected.

Conifer-associated gastropod species probably select these habitats because of deeper litter on the soil. The top most layer of litter (fallen dead plant material) offers adequate moisture retention (Moore 1986), food in the form of decaying plant material or fungal mycelia (Boycott 1934, Mason 1970), and a protective, loosely compact layer for gastropods to burrow under during periods of hot or dry weather (Boycott 1934, Burch 1955, Boag 1985). Fallen leaves of conifer take longer to breakdown than deciduous material (Daubenmire and Prusso 1963), thereby form a deeper and probably more porous layer of litter. Boag (1985) found that, under experimental conditions, snails of the genera *Vertigo*, *Discus*, and *Euconulus* spent a majority of 24 hr periods under the litter, and that greatest numbers were visible on the surface during periods of higher humidity and mild temperatures (between 6 C and 15 C). The ability to burrow into a loosely packed layer of litter is advantageous for temperature and moisture regulation (Prior 1985), compared to shallow, compact litter of strictly deciduous content that is more subject to drought (Moore 1986).

Litter depth was deep in some deer yards with high conifer components, but deer in the upper peninsula congregated in various habitat types of which litter depth was variable. So, litter depth alone does not explain why gastropods were more abundant in deer yards than in moose inhabited areas during 1996. It may also be a reflection of recent disturbance from selective logging that results in better habitat for gastropods by offering debri used for shelter. This was suggested by Gleich and Gilbert (1976) in Maine because they found gastropods more abundantly on sites that had been logged than in similar habitats that had little or no logging. Strayer *et al.* (1986) found that gastropod communities recovered very quickly in northern New England even when forest disturbance was extreme, such as clear-cut or burned areas. This reasoning, however, does not explain greater numbers of gastropods in deer yards from this study where logging did not take place (*e.g.*, artificial feeding areas).

Relative abundance of gastropods in deer yards might also be attributed to the fertilization effect of high numbers of deer defecating in a small area. Gastropods thrive in areas rich in organic nutrients (Strandine 1941, Burch 1955). The authors referred to the organic component of soil as mainly dead plant material. Fecal pellets contribute additional organic nutrients to the environment and are probably good for gastropods.

Considering that gastropods were abundant in deer yards, and deer that congregated in these areas deposited large numbers of L1s with feces, I expected greater numbers of infected gastropods in deer yards than other areas sampled. That trend was evident in both 1995 and 1996 (Figure 3-2) and even though *P*-values (> 0.05) were not significant, results suggest that focal areas of infected gastropods exist in Michigan's upper peninsula. For example, a deer yard that centered on logging in winter 1994 (site 415), had many gastropods, of which over 90% were known species of intermediate hosts, and nearly 1% of the total collected were infected (Appendix III). Deer yards in 1996 showed similar trends towards abundant gastropods of important species and higher prevalence of infection (Appendix IV). An artificial feeding area, site 404, had the greatest density of deer and high numbers of gastropods. Approximately 200 deer were fed in a 3 ha area so the ground was covered by a dense layer of deer fecal pellets. Nearly 5% of gastropods collected here were infected with *P. tenuis* which exemplifies a focal area of infected gastropods compared to many other sites.

For transmission to ungulates, focal areas must be occupied by moose and deer during snow-free seasons when gastropods are available to be ingested. Winter deer yards in the upper peninsula are mainly located at lower elevations along the edge of Lake Superior and may be of three types: 1) those centered around logging, 2) those centered on artificial feeding by private individuals, or 3) 'natural' deer yards that don't center on feeding but rather on protection from harsh weather. Deer live in and around all these areas throughout the year, although at lower numbers than in winter. Moose are seen occasionally along the edge of Lake Superior during spring and fall (Rob Aho, personal communication, personal observation). Some deer yards that center around selective logging operations (*e.g.* site 410) are more accessible to moose because they are secluded by some degree from human interaction for much of the year. Deer yards created by artificial feeding probably pose minimal risk for moose because most of these sites are close to human populated areas where moose rarely frequent. Feeding areas are more likely revisited by local deer that are undisturbed by human inhabitance. 'Natural' type deer yards are predominantly conifer habitat of northern white cedar and eastern hemlock. As determined by ordinations in this study, habitat of predominantly conifer will have some intermediate host species present but may also have many species of gastropods that don't serve as intermediate hosts such as *Euconulus fulvus, Zoogentes harpa, Striatura exigua, Striatura ferrea,* and *Punctum minitusum,* therefore limiting the importance of 'natural' deer yards for transmission. Overall, foci are probably not a major source for transmission of *P. tenuis* to either deer or moose.

Some gastropods were infected with *P. tenuis* larvae in areas inhabited by moose. Apparently resident deer, or deer travelling during spring or autumn migration, deposited L1s in areas where moose live. There is little substantial evidence that moose survive multiple infections with meningeal worm long enough to deposit larvae in their feces (see Appendix XI), therefore L1s were most likely deposited by WTD. Apparently moose are at risk of encountering *P. tenuis* within their primary range but seasonal food preferences may limit transmission to some degree.

Comparatively, moose and deer feed differently through many seasons. Diets of deer during spring, summer, and fall mostly consist of succulent ground-level foods, 63%, 79% and 79%, respectively (Skinner and Telfer 1974). These foods include herbs, grass, ferns, fruit and mast, and fungi (Skinner and Telfer 1974, Weckerly and Kennedy 1992) which could have potentially infected gastropods attached. Conversely, browse which is leaves and twigs of shrubs and trees, is consumed in greater proportions throughout the year by moose (see Renecker and Schwartz 1997) and is less likely to have gastropods attached. Browse comprised 56% of moose diets in summer and 100% during winter in the Kenai Peninsula, Alaska (LeResche and Davis 1973) and 74% in summer and 95 - 100% in winter in Alberta, Canada (Renecker 1987). Moose also eat relatively large quantities of aquatic vegetation during summer (Ritcey and Verbeek 1969, Fraser *et al.* 1984), which limits the potential for ingesting terrestrial gastropods and there is no evidence to suggest that aquatic gastropods serve as intermediate hosts in nature (Anderson 1963, Lankester and Anderson 1968). It has not been well documented whether or not moose consume ground-level vegetation along the edges of wetland habitat as well as the aquatic vegetation. If so, two intermediate host species of gastropods, *Zonitoides nitidus* and *Cionella lubrica,* allow potential for transmission if infected WTD contaminate these areas. Nonetheless, much larger proportions of ground-level vegetation are consumed by moose in autumn (Renecker and Schwartz 1997). Foods selected include forbs, sedge, grass, and relatively large quantities of leaf litter (Renecker and Hudson 1986, Renecker 1987) and all have potential for attendant terrestrial gastropods. Therefore, the seasonal shift in feeding to ground-level vegetation probably makes moose more vulnerable to infection with meningeal worm in autumn. Deer are probably more vulnerable to infection during any snow-free season because they contaminate their own environment and eat a majority of ground-level vegetation.

Risk for moose on a seasonal basis also probably varies according to age and sex. Calves are at higher risk in late summer and early autumn as they become weaned and eat greater quantities of vegetation. Schwartz (1992) found that captive reared calves began consuming solid foods at 2 - 3 wks of age. Diets of moose calves consist primarily of herbacious material by 2 months of age (Schwartz 1992, Gasaway and Coady 1974) which coincides temporally with numbers of infected gastropods found with infective L3s in my study (Table 3-7). Calves become fully weaned by mid-September (Dodds 1959, Schwartz 1992). Females are at risk during autumn because they feed regularly to prepare for winter (Schwartz *et al.* 1984) and utilize ground-level foods as described previously. Breeding bulls, during the late summer- early autumn rut, reduce food intake or cease eating altogether up to 18 days (Schwartz *et al.* 1984), therefore, adult males are at lower risk during early autumn than calves or females. Male moose, however, are probably susceptible to acquiring *P. tenuis* during spring; particularly young males that are shunned by mothers during May and disperse further than their female counterparts (Cederlund *et al.* 1987). Spring may be a particularly vulnerable season for young moose in the upper peninsula that leave the primary range and encounter areas of higher deer density. High numbers of deer may contaminate areas with infected feces, resulting in greater risks for moose to encounter infected gastropods, especially if they wander through deer yards from the previous winter.

Although data from this study suggest that most transmission to ungulates occurs in late summer and autumn, spring transmission is possible. Infective L3s were found in gastropods collected in June. These gastropods almost certainly survived the previous winter. This phenomenon has been reported previously for *P. tenuis*; L3s have been found in gastropods as early as May (Lankester and Anderson 1969, Platt 1989). The low percentage of infected gastropods in October, 1995, was probably because lower than normal temperatures induced important intermediate host species to become dormant. Higher mean numbers of infective L3s found in 1996 probably reflect the sampling of greater numbers of lowland sites and deer yards with higher densities of WTD (*i.e.*, site 404).

In summary, although few species of gastropods were found infected in the upper peninsula, many of the most wide-ranging species were important intermediate hosts for *P. tenuis*. Two species because of their affinity for wet and sunny habitats, *Zonitoides nitidus* and *Cionella lubrica*, are intermediate host species more likely than others to be found around the edges of wetland areas where moose often feed during summer. Overall, all habitat types probably have potential for transmission if infected WTD are present because potential intermediate hosts are common and relatively abundant.

Evidence suggests that deer yards can serve as focal areas of infected gastropods, but are not primary sources for transmission to ungulate hosts because of 1) the limited use of these areas by deer and moose during snow free seasons, 2) the small scattered pockets of infected gastropods that could be missed by passing ungulates, and 3) the variation in numbers of infected gastropods between different deer yards.

Intermediate host gastropods are present in the preferred habitats for moose in the upper peninsula, therefore moose are at risk to acquire *P. tenuis* within their own range. In general, moose are probably most vulnerable during autumn because of changes in diet. Although, young male moose may be equally vulnerable during spring because of their wandering nature that could lead them to more highly contaminated areas. Moose calves could be highly susceptible to late-summer and autumn transmission because of progressive weaning. Overall, random and low-level infections are probably the most common scenario for transmission of *P. tenuis* to moose and deer of Michigan's upper peninsula.

Table 3-1. Total numbers of gastropods (Gastropoda: Pulmonata) collected in 1995 and 1996 by species. Classification after Burch and Pearce (1990).

	Number Collected			% Relative
Species	1995	1996	Total	Abundance
Order Geophila				
Suborder Sigmaurethra				
Family Discidae				
Discus spp.*	860	726	1586	17
Anguispira alternata	225	161	386	4
Family Helicodiscidae				
Helicodiscus parallelus	66	44	110	1
Family Vitrinidae				
Zonitoides arboreus	2111	1344	3455	37
Zonitoides nitidus	152	91	243	3
Nesovitrea electrina	12	42	54	0.6
Striatura exigua	408	71	479	5
Striatura ferrea	53	7	60	0.7
Vitrina limpida	1	19	20	0.2
Family Limacidae				
Deroceras laeve	426	241	667	7
Deroceras reticulatum	120	103	223	2
Family Punctidae				
Punctum minitusum	91	8	99	1
Family Philomycidae				
Pallifera dorsalis	232	131	363	4
Family Mesodontidae				
Immature Mesodontidae	15	35	50	0.5
Triodopsis albolabris	7	6	13	0.1
Strenotrema fraternum	10	10	20	0.2
Family Euconulidae				
Euconulus fulvus	96	14	110	1
Suborder Orthuretha				
Family Cionellidae				
Cionella lubrica	809	476	1285	14
Family Vallonidae				
Zoogenetes harpa	36	3	39	0.4
Vallonia excentrica	0	7	7	0.1
Family Pupillidae				
Columella edentula	5	0	5	0.1
Vertigo tridentata	41	1	42	0.1
Family Strobilopsidae				
Strobilops labyrinthica	125	111	236	3
TOTAL	5901	3651	9552	

* *Discus* spp. = *Discus cronkhitei* and *Discus catskillensis*

Table 3-2. Prevalence of infected gastropods from repeat collection sites between 10 June and 12 August for 1995 and 1996.

	Number Collected		Number Infected		Prevalence (%)		Number Species	
Site	1995	1996	1995	1996	1995	1996	1995	1996
212	346	571	1	1	0.3	0.2	10	9
225	128	171	0	0	0	0	14	11
631	312	233	0	0	0	0	7	7
632	154	131	0	1	0	0.8	6	13

Table 3-3a. Summary of canonical correspondence analysis of 22 sites where gastropod and vegetative species data were collected in 1995, and five environmental variables.

Axis	1	2	3	4
Eigenvalue	0.30	0.17	0.12	0.10
Species/Environment Correlation	0.93	0.92	0.94	0.92
Cumulative % Variance of				
Species Data Explained	12.6	19.4	24.4	28.4
Species-Environment Relation	39.7	61.4	77.3	89.8

Table 3-3b. Statistics for environmental variables used in canonical correspondence analysis of 22 sites where gastropod and vegetative species data were collected in 1995. Asterisks indicate significance at $P \leq 0.05$. Absolute *t*-values ≥ 2.1 (d.f. = 16) indicate important canonical coefficients (ter Braak 1987). Bold values indicate important variables with significant correlation and canonical coefficients.

	Interset Correlations		Canonical Coefficients		t - values	
Variables	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Canopy Cover	**-0.84**	-0.30	-0.95*	-0.26*	-8.40*	-2.21*
Soil Depth	-0.46	0.41	-0.36*	0.81*	-3.09*	6.64*
Soil Type	-0.18	**-0.64**	0.01	-0.40*	0.08	-2.17*
Permeability	-0.15	**-0.52**	0.32	-0.44*	1.80	-2.35*
Water Table	-0.10	-0.17	-0.23	-0.12	-1.98	-1.01

Table 3-4a. Summary of canonical correspondence analysis of 13 sites where gastropod and vegetative species data were collected in 1996, and five environmental variables.

Axis	1	2	3	4
Eigenvalue	0.45	0.24	0.14	0.13
Species/Environment Correlation	0.97	0.97	0.96	0.89
Cumulative % Variance of				
Species Data Explained	22.6	34.6	41.4	47.8
Species-Environment Relation	42.5	64.8	77.6	89.7

Table 3-4b. Statistics for environmental variables used in canonical correspondence analysis of 13 sites where gastropod and vegetative species data were collected in 1996. Asterisks indicate significance at $P \leq 0.05$. Absolute *t*-values ≥ 2.37 (d.f. = 7) indicate important canonical coefficients (ter Braak 1987). Bold values indicate important variables with significant correlation and canonical coefficients.

	Interset Correlations		Canonical Correlations		t - values	
Variables	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Canopy Cover	**-0.95**	-0.07	-0.95*	0.43*	-8.80*	3.82*
Soil Depth	-0.46	**0.77**	-0.12	-0.69*	-0.94	-5.13*
Soil Type	-0.12	-0.69	0.21	-0.18	1.43	-1.16
Permeability	-0.22	-0.72	-0.17	-0.34	-1.23	-2.30
Water Table	-0.04	-0.48	0.01	-0.07	0.08	-0.63

Table 3-5. Numbers of gastropods collected and infected with *Parelaphostrongylus tenuis*, by species in 1995 and 1996.

	Number Collected			Number Infected			Prevalence (%)			Intensity (Mean)		
Species	1995	1996	Total	1995	1996	Total	1995	1996	Total	1995	1996	Total
Order Geophila												
Suborder Sigmaurethra												
Family Discidae												
Discus spp.*	854	704	1558	11	15	26	1.3	2.1	1.7	1.2	1.7	1.5
Anguispira alternata	225	161	386	1	3	4	0.4	1.9	0.8	1.0	4.3	3.5
Family Helicodiscidae												
Helicodiscus parallelus	66	44	110	0	0	0	0	0	0	0	0	0
Family Vitrinidae												
Zonitoides arboreus	2102	1317	3419	5	8	13	0.2	0.6	0.4	1.0	1.0	1.0
Zonitoides nitidus	149	91	240	3	1	4	2.0	1.1	1.7	3.3	8.0	4.5
Nesovitrea electrina	12	42	54	0	0	0	0	0	0	0	0	0
Striatura exigua	408	71	479	0	0	0	0	0	0	0	0	0
Striatura ferrea	53	7	60	0	0	0	0	0	0	0	0	0
Vitrina limpida	1	19	20	0	0	0	0	0	0	0	0	0
Family Limacidae												
Deroceras laeve	424	236	660	4	5	9	0.9	2.1	1.4	1.0	4.0	2.7
Deroceras reticulatum	120	103	223	0	0	0	0	0	0	0	0	0
Family Punctidae												
Punctum minitusum	91	8	99	0	0	0	0	0	0	0	0	0

(Continued)

Table 3-5. Continued

Species	Number Collected			Number Infected			Prevalence (%)			Intensity (Mean)		
	1995	1996	Total	1995	1996	Total	1995	1996	Total	1995	1996	Total
Family Phylomycidae												
Pallifera dorsalis	232	131	363	3	2	5	1.3	1.5	1.4	1.7	2.0	1.8
Family Mesodontidae												
Immature Mesodontidae	15	35	50	0	0	0	0	0	0	0	0	0
Triodopsis albolabris	7	6	13	2	4	6	29	67	46	1.0	7.5	5.3
Strenotrema fraternum	10	10	20	0	0	0	0	0	0	0	0	0
Family Euconulidae												
Euconulus fulvus	96	14	110	0	0	0	0	0	0	0	0	0
Suborder Orthurethra												
Family Cionellidae												
Cionella lubrica	808	476	1284	1	0	1	0.1	0	0.1	1.0	0	1.0
Family Vallonidae												
Vallonia excentrica	0	7	7	0	0	0	0	0	0	0	0	0
Zoogenetes harpa	36	3	39	0	0	0	0	0	0	0	0	0
Family Pupillidae												
Columella edentula	5	0	5	0	0	0	0	0	0	0	0	0
Vertigo tridentata	41	1	42	0	0	0	0	0	0	0	0	0
Family Strobilopsidae												
Strobilops labrynthica	125	111	236	0	0	0	0	0	0	0	0	0
Total	5880	3597	9477	30	38	68	0.5	1.1	0.7	1.4	2.9	2.2

**Discus* spp. = *Discus cronkhitei* and *Discus catskillensis*

Table 3-6. Measurements of larvae identified as *Parelaphostrongylus tenuis* in 1995 and 1996 compared to previously published results. Ranges are in parentheses. All measurements are in µm unless stated otherwise. Characteristics of small larvae (< 800 µm) were measured as percent total body lengths.

	Anderson (1963)		Ballantyne and Samuel (1984)	This Study
	L2s	L3s	L3s	L2s and L3s
Total Length	715	971 (900 - 1080)	1200 (1100 - 1323)	837 (700 - 1155)
Nerve Ring	101	114 (100 - 125)	165 (152 - 174)	111 (73 - 151)
% Total Body Length	14	12 (10 - 13)	---	13 (10 - 15)
Excretory Pore	113	133 (122-149)	---	118 (81 - 155)
% Total Body Length	16	14 (12 - 15)	---	14 (12 - 15)
Oesophagus	242	352 (300 - 400)	463 (421-521)	323 (223 - 458)
% Total Body Length	34	36 (34 - 41)	---	37 (33 - 42)

Table 3-7. Numbers of intermediate host gastropods and infective L3s collected by month, 1995 and 1996. Numbers include seven species. *Cionella lubrica* is not included because of low prevalence.

	Intermediate Host Species				Larvae			
	Total Number Examined		Percent Infected with L3s		Mean Number of Infective L3s (±s.d.)		Percent of Total Larvae Infective L3s	
	1995	1996	1995	1996	1995	1996	1995	1996
June	764*	711*	0.26	0.70	1.0 (0.0)	1.7 (1.0)	100	70
July	1359	1512	0.74	0.79	0.7 (0.5)	2.2 (3.7)	80	51
August	1534	477**	0.65	4.40	1.3 (1.1)	2.5 (2.3)	72	80
September	672	---	0.74	---	0.9 (0.7)	---	86	---
October	493***	---	0.41	---	0.3 (0.6)	---	33	---

* None collected before 5 and 10 June, respectively

** None collected after 12 August

*** None collected after 11 October

Table 3-8. Index of parasite abundance values calculated for intermediate host species collected in 1995 and 1996. Values account for relative abundance of species.

Species	Index of Parasite Abundance
Suborder Sigmurethra	
Family Discidae	
Discus spp. *	0.421
Anguispira alternata	0.277
Family Mesodontidae	
Triodopsis albolabris	0.246
Family Vitrinidae	
Zonitoides arboreus	0.143
Zonitoides nitidus	0.084
Family Limacidae	
Deroceras laeve	0.090
Family Phylomycidae	
Pallifer dorsalis	0.013
Suborder Orthurethra	
Family Cionellidae	
Cionella lubrica	0.004

* *Discus* spp. = *Discus cronkhitei* and *Discus catskillensis*

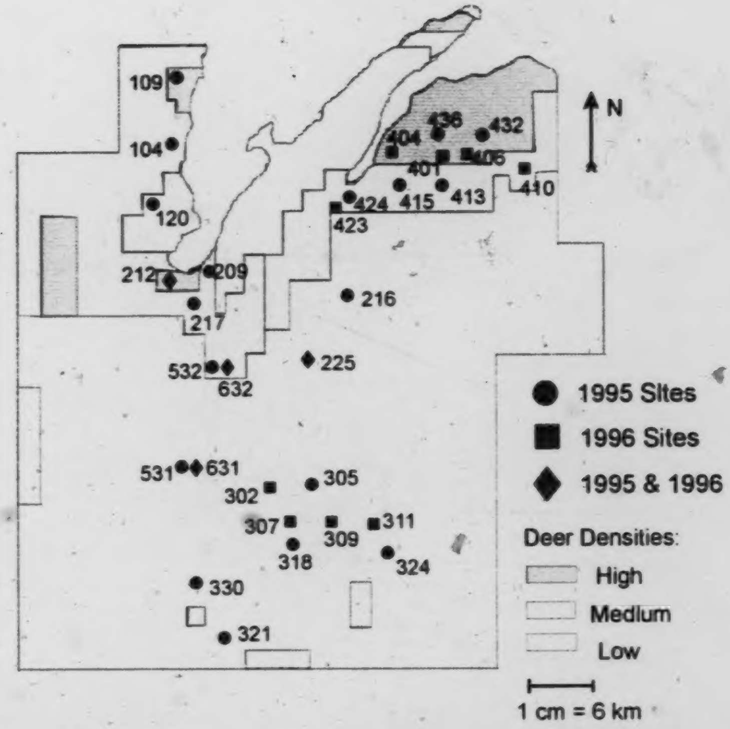

109
104
120
212
209
217
532
632
225
216
424
423
415
413
404
436
432
401
406
410
531
631
302
305
307
309
311
318
324
330
321
N
1995 Sites
1996 Sites
1995 & 1996
Deer Densities:
High
Medium
Low
1 cm = 6 km

Figure 3-1. Gastropod collection sites for 1995 and 1996 that include designated deer density areas determined by Michigan Department of Natural Resources for winter 1994. High = ≥ 12 deer/km^2, Medium = 6 – 11 deer/km^2, Low = ≤ 5 deer/km^2.

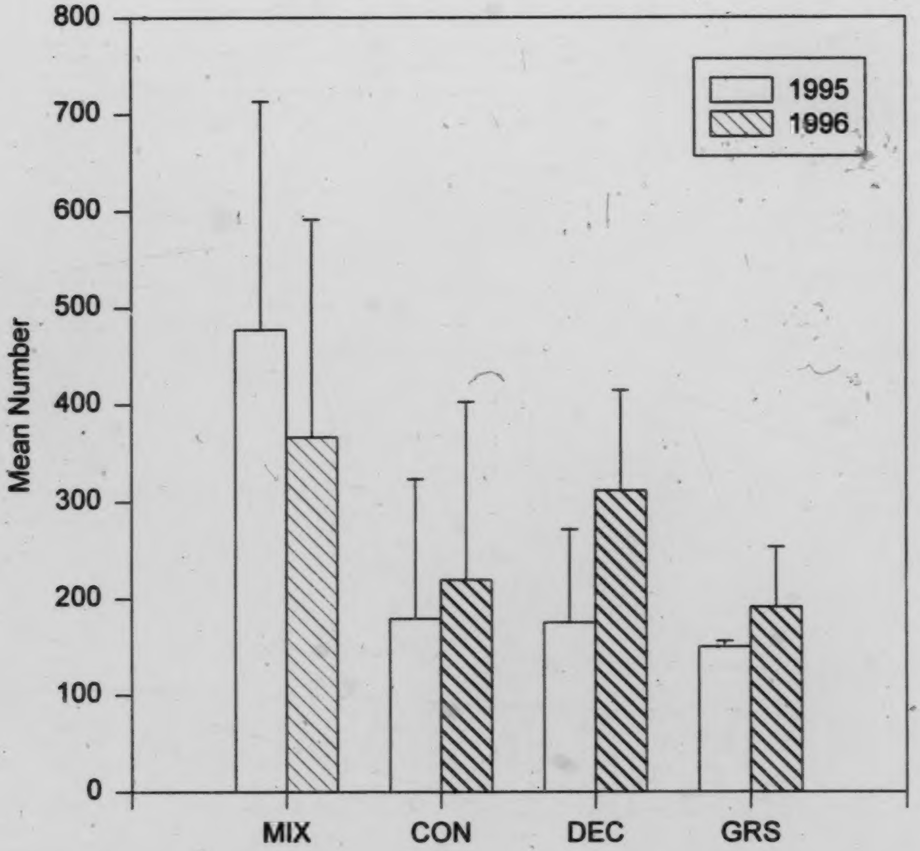


Figure 3-2. Numbers of gastropods collected by habitat type in 1995 and 1996. Bars represent one standard deviation. MIX = Mixed conifer-deciduous, CON = Predominantly Conifer, DEC = Predominantly Deciduous, GRS = Grass.

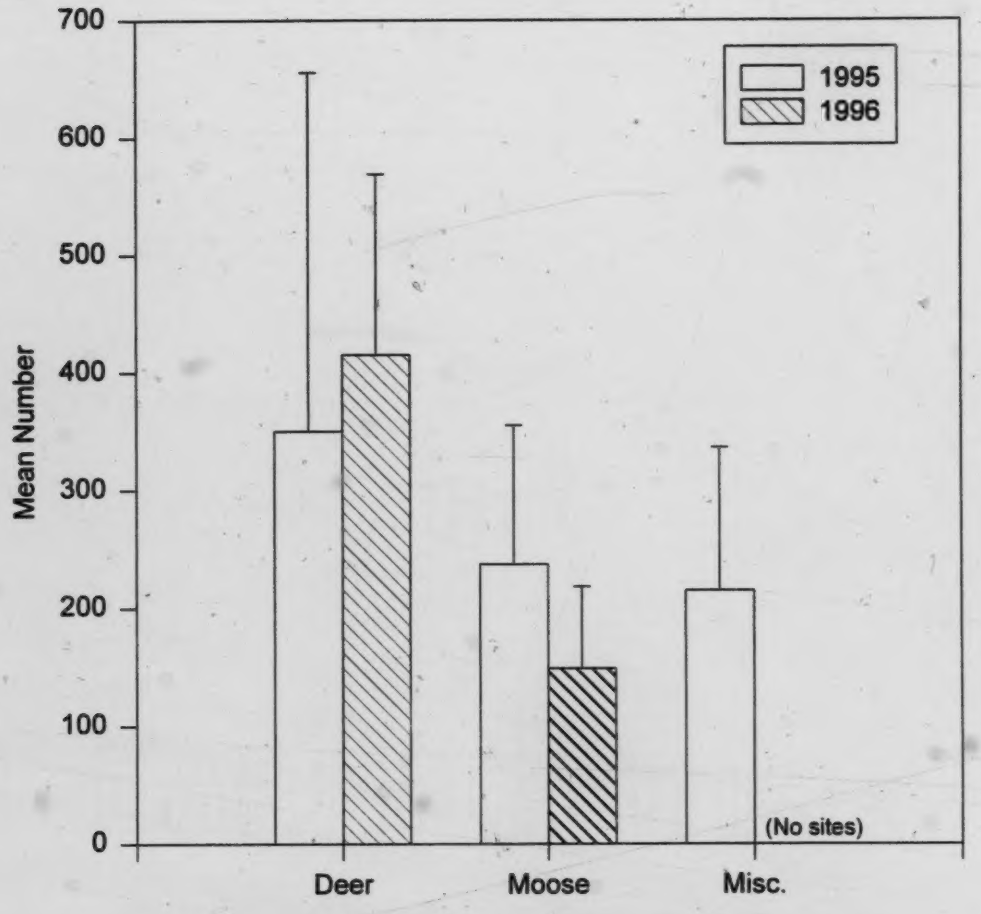


Figure 3-3. Numbers of gastropods collected by categories in 1995 and 1996. Bars represent one standard deviation. Deer = Areas where deer congregated, Moose = Areas where moose inhabited, Misc. = Miscellaneous areas.

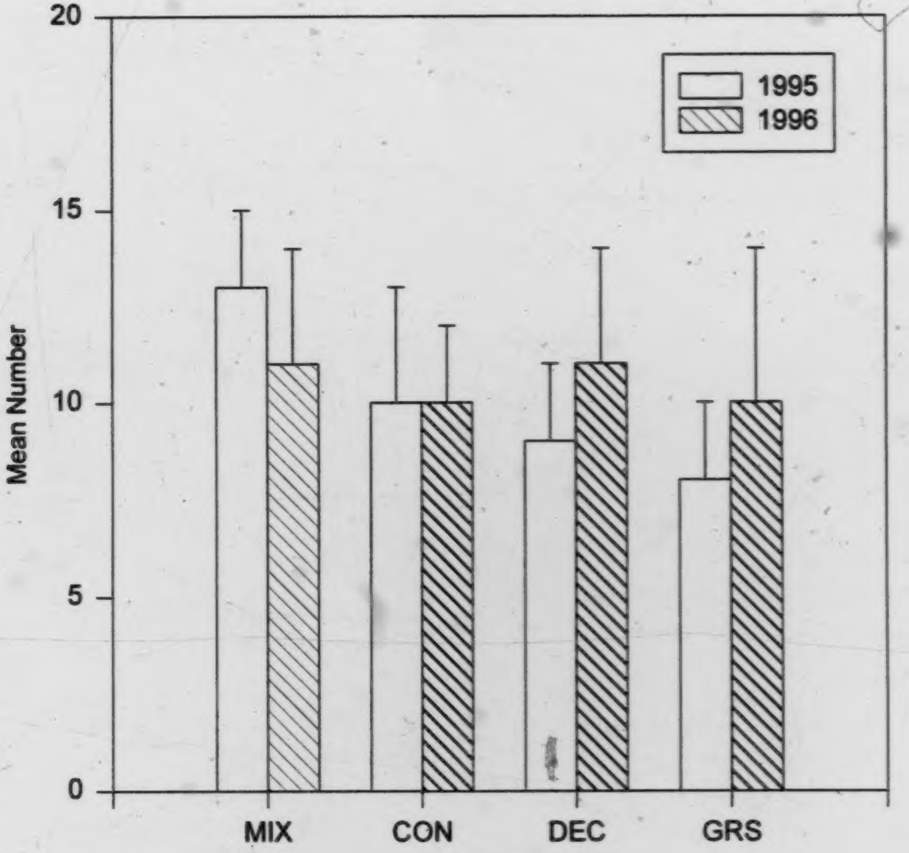


Figure 3-4. Number of species of gastropods collected by habitat type in 1995 and 1996. Bars represent one standard deviation. MIX = Mixed Conifer-deciduous, CON = Predominantly Conifer, DEC = Predominantly Deciduous, GRS = Grass.

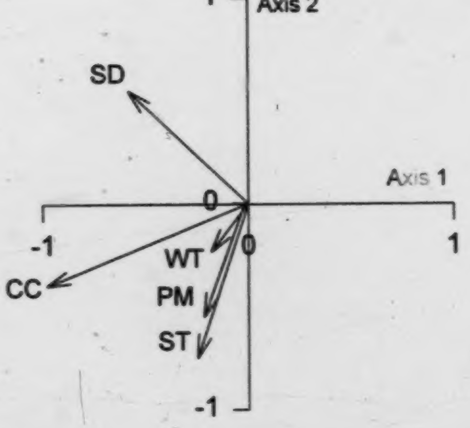


Figure 3-5a. Environmental variables used in canonical correspondence analyses for 1995. CC = Canopy Cover, PM = Permeability, SD = Soil Depth, ST = Soil Type, WT = Depth of Watertable.

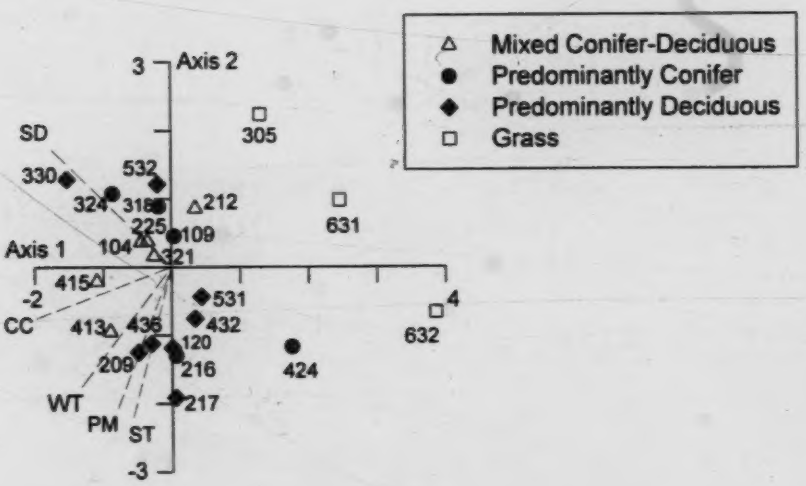
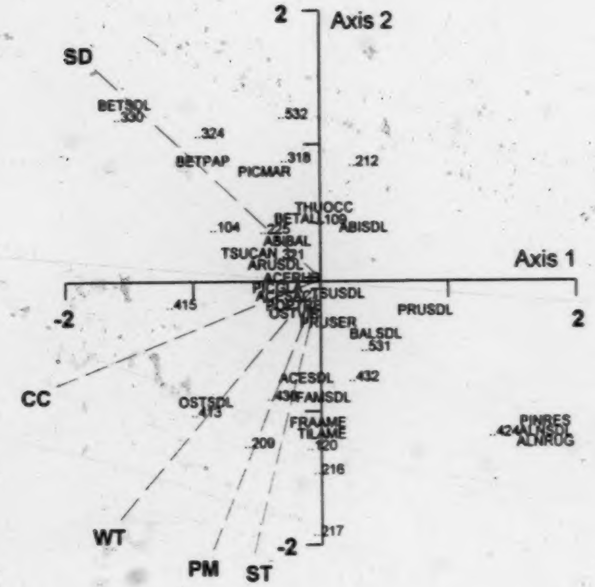


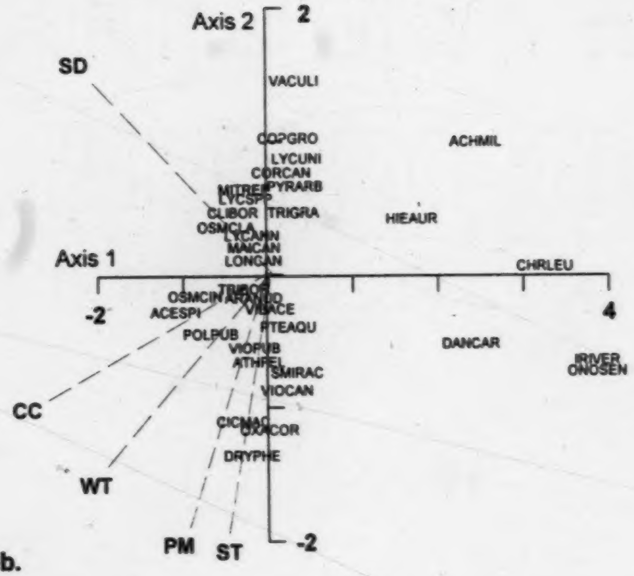
Figure 3-5b. Site distributions including habitat types from canonical correspondence analyses, 1995. Dotted lines show angles of corresponding environmental variables. Refer to Figure 3-9a for abbreviations.

Figure 3-6a. Ordination showing spatial distribution of tree species and seedlings in relation to collection sites and environmental variables, 1995. Dotted lines show angles of environmental variables, refer to Figure 3-9a for abbreviations. Refer to Appendix VIIIa-c for abbreviations of species names.

Figure 3-6b. Ordination showing spatial distribution of plant species in relation to environmental variables, 1995. Dotted lines show angles of environmental variables, refer to Figure 3-9a for abbreviations. Refer to Appendix VIIIa-c for abbreviations of species names.


2
Axis 2
SD
BETSDL
..330
..324
..532
BETPAP
PICMAR
..318
.212
THUOCC
BETALL109
ABISDL
..104
..225
ABIBAL
TSUCAN 321
ARUSDL
Axis 1
-2
.415
TSUSDL
PRUSDL
2
PRUSER
BALSDL
..531
CC
ACESDL
..432
OSTSDL
..413
FAMSDL
FRAAME
TILAME
..120
PINRES
..424ALNSDL
ALNRUG
..209
..216
WT
..217
-2
PM
ST

3-6a.


Axis 2
2
SD
VACULI
COPGRO
ACHMIL
LYCUNI
CORCAN
MITREP
PYRARB
LYCSPP
CLIBOR
TRIGRA
HIEAUR
OSMCLA
LYCANN
MAICAN
LONCAN
Axis 1
CHRLEU
TRIBOR
OSMCIN
ACESPI
VIBACE
-2
4
PTEAQU
POLPUB
DANCAR
VIOPUB
ATHFEL
IRIVER
ONOSEN
SMIRAC
CC
VIOCAN
CICMAC
OXACOR
DRYPHE
WT
PM
ST
-2

3-6b.

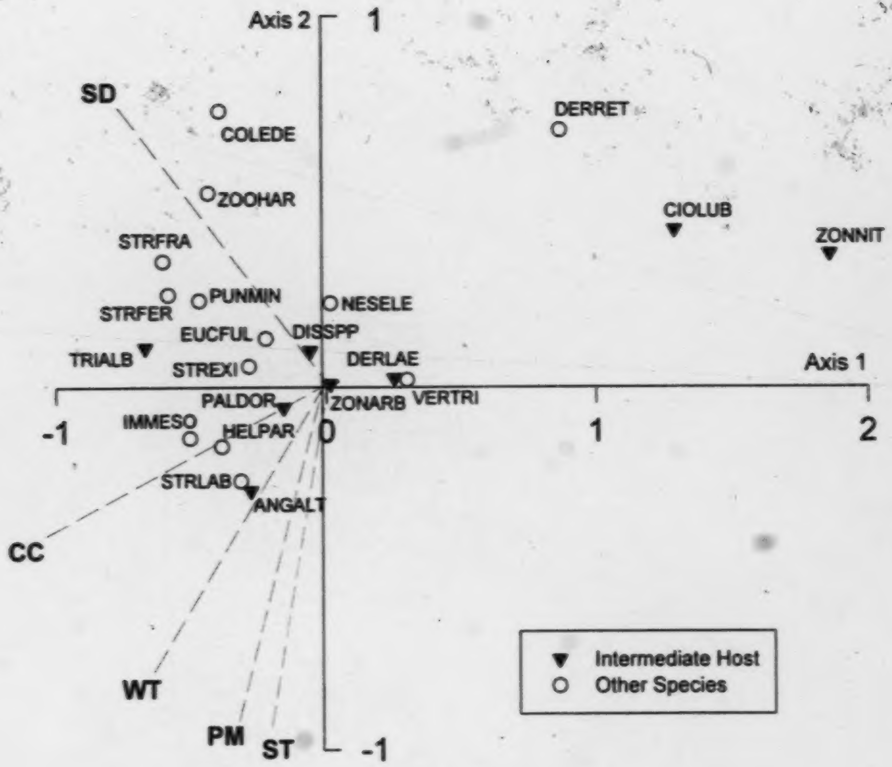


Figure 3-7. Ordination showing spatial distribution of gastropod species in relation to environmental variables, 1995. Dotted lines show angles of environmental variables, refer to figure 3-9a for abbreviations. Refer to appendix VII for abbreviations of species names.

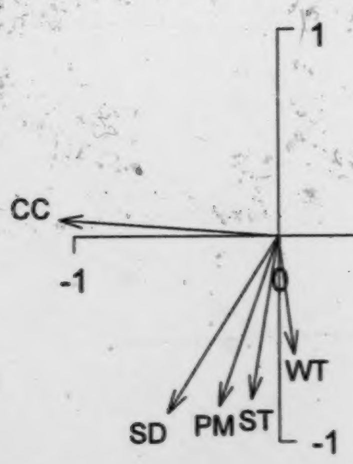


Figure 3-8a. Environmental variables used in canonical correspondence analyses for 1996. CC = Canopy Cover, PM = Permeability, SD = Soil Depth, ST = Soil Type, WT = Depth of Water Table.

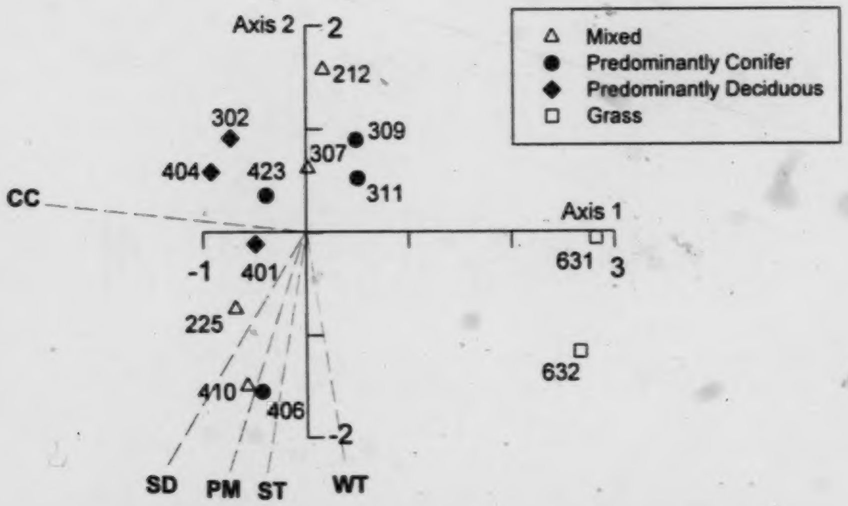
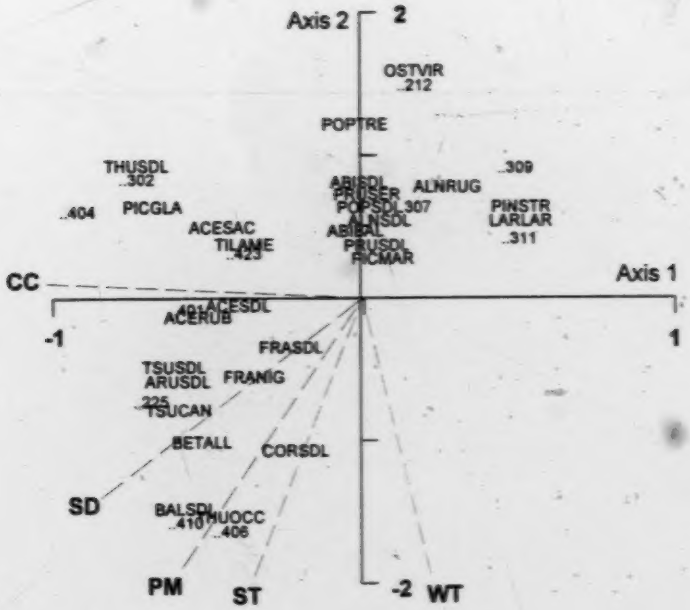


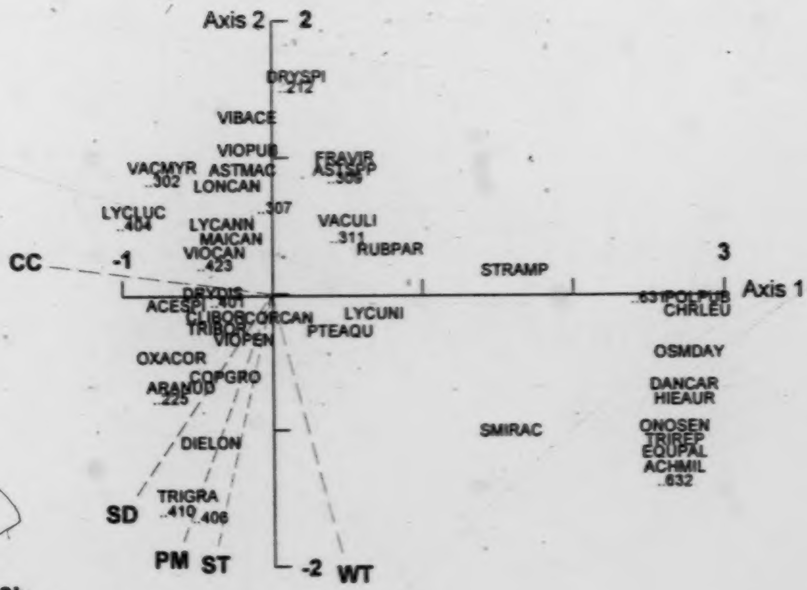
Figure 3-8b. Site distributions including habitat types from canonical correspondence analyses, 1996. Dotted lines show angles of environmetal variables, refer to Figure 3-12a for abbreviations.

Figure 3-9a. Ordination showing spatial distribution of tree and seedling species in relation to sites and environmental variables, 1996. Dotted lines show angles of environmental variables, refer to Figure 3-12a for abbreviations. Refer to Appendix VIIIa-c for abbreviations of species names.

Figure 3-9b. Ordination showing spatial distribution of plant species in relation to environmental variables, 1996. Dotted lines show angles of environmental variables, refer to Figure 3-12a for abbreviations. Refer to Appendix VIIIa-c for abbreviations of species names.


Axis 2
2
OSTVIR
..212
POPTRE
THUSDL
..302
..309
ABISDL
PRUSER
ALNRUG
POPSDL
..307
..404
PICGLA
ALNSDL
PINSTR
LARLAR
ACESAC
ABIBAL
..311
TILAME
..423
PRUSDL
PICMAR
CC
Axis 1
..401
ACESDL
ACERUB
-1
1
FRASDL
TSUSDL
ARUSDL
FRANIG
..225
TSUCAN
BETALL
CORSDL
SD
BALSDL
..410
THUOCC
..406
PM
ST
-2
WT

3-9a.


Axis 2
2
DRYSPI
..212
VIBACE
VIOPUB
FRAVIR
VACMYR
ASTMAC
ASTSPP
..309
..302
LONCAN
..307
LYCLUC
..404
LYCANN
VACULI
MAICAN
..311
CC
-1
VIOCAN
RUBPAR
..423
3
STRAMP
Axis 1
DRYDIS
..401
..631
POLPUB
CHRLEU
ACESPI
CLIBOR
CORCAN
LYCUNI
TRIBOR
VIOPEN
PTEAQU
OXACOR
OSMDAY
COPGRO
ARANUD
..225
DANCAR
HIEAUR
DIELON
SMIRAC
ONOSEN
TRIREP
EQUPAL
ACHMIL
..632
TRIGRA
SD
..410
..406
PM
ST
-2
WT

3-9b.

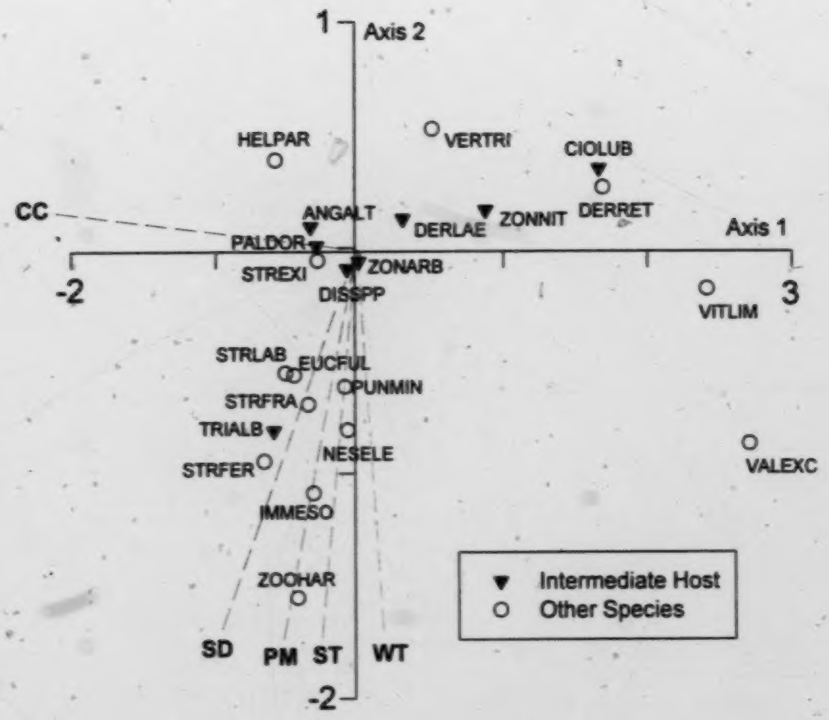


Figure 3-10. Ordination showing spatial distribution of gastropod species in relation to environmental variables, 1996. Dotted lines show angles of environmental variables, refer to Figure 3-12a for abbreviations. See Appendix VII for abbreviations of species names.

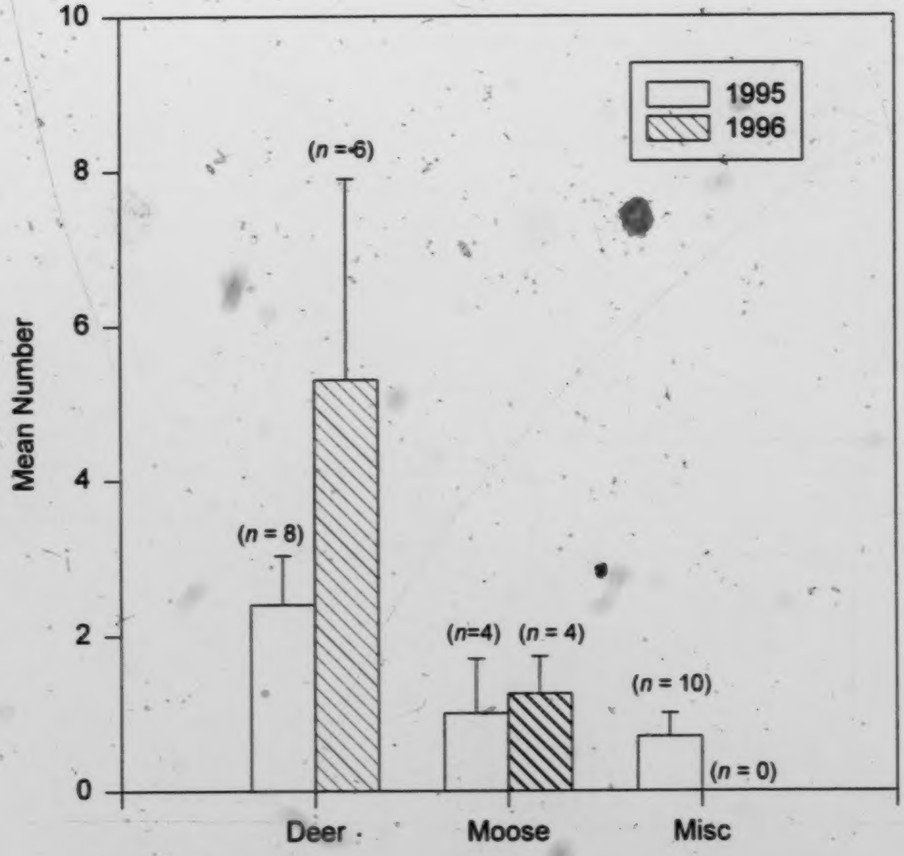
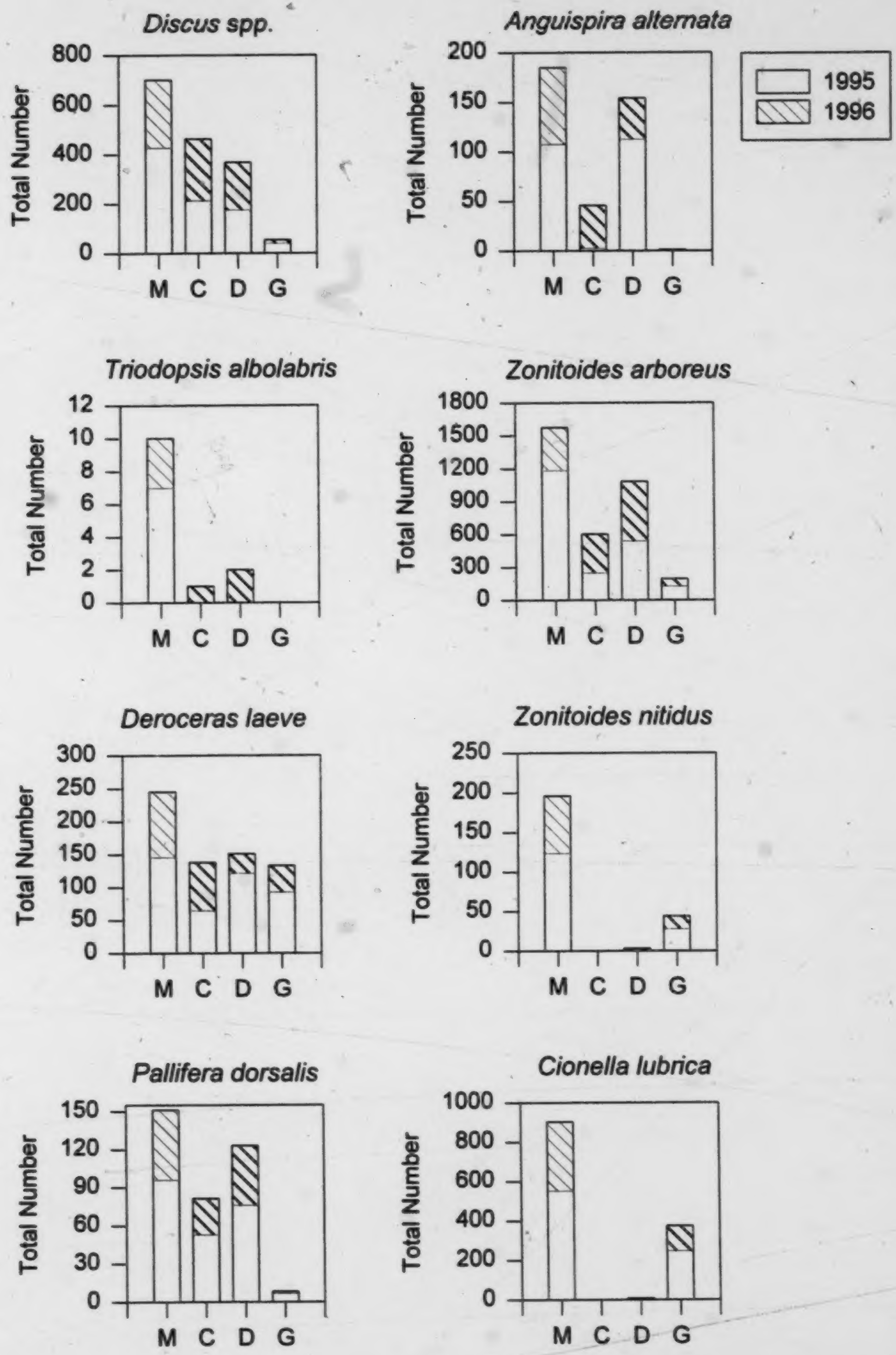


Figure 3-11. Numbers of infected gastropods by host-use categories in 1995 and 1996. Bars represent one standard error. Deer = Areas where deer congregated, Moose = Areas where moose inhabited, Misc = Miscellaneous areas. (*n* = number of sites)

Figure 3-12. Numbers of gastropods which are known intermediate hosts for *Parelaphostrongylus tenuis*, collected by habitat type in 1995 and 1996. M = Mixed Conifer-Deciduous, C = Predominantly Conifer, D = Predominantly Deciduous, G = Grass.



Discus spp.
Total Number
0
200
400
600
800
M
C
D
G
Anguispira alternata
Total Number
0
50
100
150
200
M
C
D
G
1995
1996
Triodopsis albolabris
Total Number
0
2
4
6
8
10
12
M
C
D
G
Zonitoides arboreus
Total Number
0
300
600
900
1200
1500
1800
M
C
D
G
Deroceras laeve
Total Number
0
50
100
150
200
250
300
M
C
D
G
Zonitoides nitidus
Total Number
0
50
100
150
200
250
M
C
D
G
Pallifera dorsalis
Total Number
0
30
60
90
120
150
M
C
D
G
Cionella lubrica
Total Number
0
200
400
600
800
1000
M
C
D
G

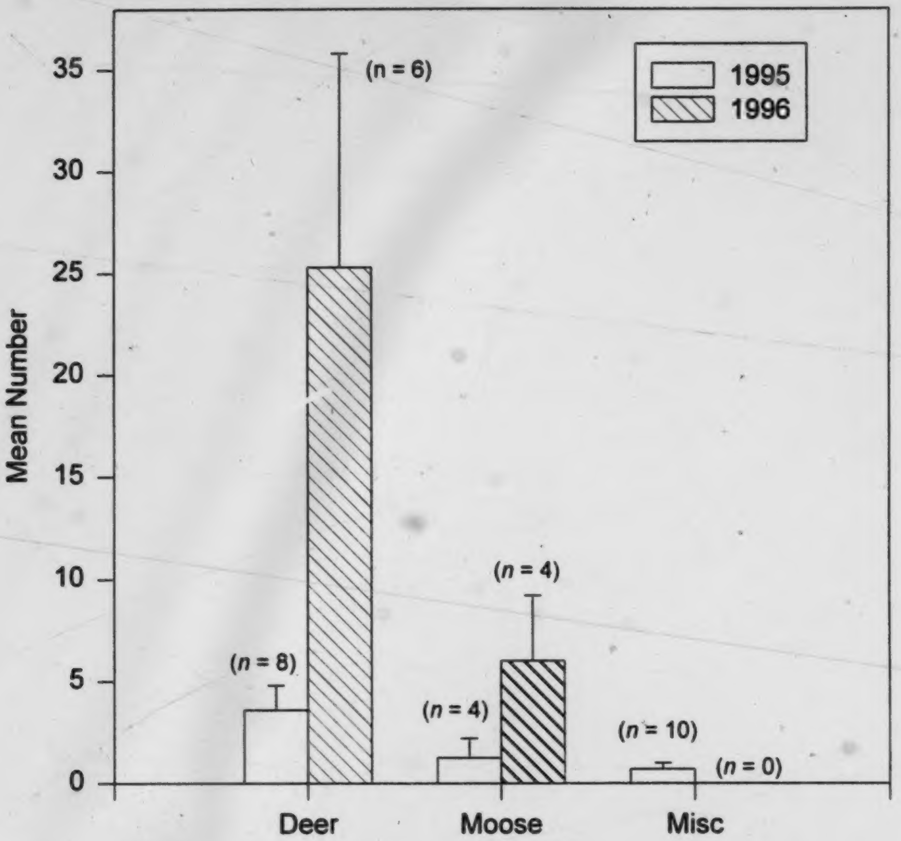


Figure 3-13. Number of larvae (L2s and L3s) in gastropods by host-use categories in 1995 and 1996. Bars represent one standard error. Deer = Areas where deer congregated, Moose = Areas where moose inhabited, Misc = Miscellaneous areas. (*n* = number of sites per category)

Literature Cited

Aho, R. W. 1995. Michigan's translocated moose population: 10 years later. Michigan Department of Natural Resources WildlifeDivision Report Number 3245. 18 pp.

Anderson, R.C. 1963. Studies on *Pneumostrongylus tenuis* Dougherty, 1945 of *Odocoileus virginianus*. The Journal of Parasitology 49: 47.

Andersen, J. and O. Halvorsen. 1984. Species composition, abundance, habitat requirements and regional distribution of terrestrial gastropods in arctic Norway. Polar Biology 3: 45-53.

Anderson, R.C. and A.K. Prestwood. 1981. Lungworms. Pages 266-317 *In* Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.), Diseases and parasites of white-tailed deer. Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida. 458 pp.

Ballentyne, R.J. and W.M. Samuel. 1984. Diagnostic morphology of the third-stage larvae of three species of *Parelaphostrongylus* (Nematoda, Metastrongyloidea). The Journal of Parasitology 70: 602-604.

Barnes, B.V. and W.H. Wagner, Jr. 1981. Michigan trees: a guide to the trees of Michigan and the Great Lakes Region. The University of Michigan Press, Ann Arbor, Michigan. 383 pp.

Bartlett, I.H. 1950. Michigan deer. (Bulletin) Michigan Department of Conservation, Lansing, Michigan. 11 pp.

Berndt, L.W. 1988. Soil survey of Baraga County area, Michigan. United States Department of Agriculture, Washington D.C. 306 pp.

Boag, D.A. 1982. Overcoming sampling bias in studies of terrestrial gastropods. Canadian Journal of Zoology 60: 1289-1292.

-------- 1985. Microdistribution of three genera of small terrestrial snails (Stylommatophora: Pulmonata). Canadian Journal of Zoology 63: 1089-1095.

-------- 1990. On the effectiveness of artificial shelters in the study of population attributes of small terrestrial gastropods. Canadian Journal of Zoology 68: 254-262.

Boycott, A.E. 1934. The habitats of land mollusca in Britain. Journal of Ecology 22: 1-38.

Burch, J.B. 1955. Some ecological factors of the soil affecting the distribution and abundance of land snails in eastern Virginia. The Nautilus 69: 62-69.

-------- 1962. How to know the eastern land snails. William C. Brown Company Publishers, Dubuque, Iowa. 214 pp.

Burch, J.B. and Y. Jung. 1988. Land snails of the University of Michigan Biological Station area. Walkerana (Volume 3, Number 9). 177 pp.

Burch, J.B. and T.A. Pierce. 1990. Terrestrial gastropoda. Pages 201 - 310 *In* D. Dindal (ed.), Soil Biology Guide. John Wiley & Sons, Inc., New York, New York. 1295 pp.

Cederlund, G., F. Sandegren, K. Larsson. 1987. Summer movements of female moose and dispersal of their offspring. The Journal of Wildlife Management 51: 342-352.

Clarke, A.H., J.P. Kelsall, and G.R. Parker. 1968. The land snail fauna of Fundy National Park, New Brunswick. National Museum of Canada: Contributions to Zoology, Bulletin IV 223: 5-22.

Daubenmire, R. and D.C. Prusso. 1963. Studies of the decomposition rates of tree litter. Ecology 44: 589-592.

Dodds, D.G. 1959. Feeding and growth of a captive moose calf. The Journal of Wildlife Management 23: 231-232.

Fraser, D., E.R. Chavez, and J.E. Paloheimo. 1984. Aquatic feeding by moose: selection of plant species and feeding areas in relation to plant chemical composition and characteristics of lakes. Canadian Journal of Zoology 62: 80-87.

Gasaway, W.C. and J.W. Coady. 1974. Review of energy requirements and rumen fermentation in moose and other ruminants. Naturaliste Canadien 101: 227-262.

Getz, L.L. 1959. Notes on the ecology of slugs: *Arion circumscriptus*, *Deroceras reticulatum*, and *D. laeve*. The American Midland Naturalist 61: 485-498.

-------- 1974. Species diversity of terrestrial snails in the Great Smoky Mountains. The Nautilus 88: 6-9.

Getz, L.L. and L.F. Chichester. 1971. Introduced European slugs. The Biologist 53: 118-127.

Gleich, J.G. and F.F. Gilbert. 1976. A survey of terrestrial gastropods from central Maine. Canadian Journal of Zoology 54: 620-627.

Gleich, J.G., F.F. Gilbert, and N.P. Kutscha. 1977. Nematodes in terrestrial gastropods from central Maine. Journal of Wildlife Diseases 13: 43-46.

Hawkins, J.W., S. Newmaster, M.W. Lankester, K.W. Watt, F.W. Bell, and R.A. Lautenschlager. 1998. Terrestrial gastropod distribution in relation to vegetation and soil characteristics in northwestern Ontario. Unpublished manuscript. 25 pp.

Kearney, S.R. and F.F. Gilbert. 1978. Terrestrial gastropods form the Himsworth Game Preserve, Ontario, and their significance in *Parelaphostrongylus tenuis* transmission. Canadian Journal of Zoology 56: 688-694.

Kent, M. and P. Coker. 1996. Vegetation description and analysis, a practical approach. John Wiley & Sons, Inc., New York, New York. 363 pp.

Lankester, M.W. and R.C. Anderson. 1968. Gastropods as intermediate hosts of *Pneumostrongylus tenuis* Dougherty of white-tailed deer. Canadian Journal of Zoology 46:373-383.

-------- and W.J. Peterson. 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. Journal of Wildlife Diseases 32: 31-38.

Lankester, M.W. and W.M. Samuel. 1997. Pests, parasites and diseases. Pages 479-517 *In* C.C. Schwartz and A.W. Frazmann (eds.), Ecology and Management of the North American Moose. A Wildlife Management Institute Book, Smithsonian Institution Press, Washington D.C. 733 pp.

Latchford, F.R. 1885. Observations on the terrestrial mollusca of Ottawa and vicinity. Transactions of the Ottawa Field-Naturalists' Club 2: 211-231.

Lee, C.B. 1952. Ecological aspects of Stenotrema hirsutum (Say) in the region of Ann Arbor, Michigan. The American Midland Naturalist 47: 55-60.

Leong, T.S. 1975. Metazoan parasites of fishes of Cold Lake, Alberta: a community analysis. Ph.D. thesis, Department of Zoology, University of Alberta, Edmonton. 170 pp.

LeResche, R.E. and J.L. Davis. 1973. Importance of non-browse foods to moose on the Kenai Peninsula, Alaska. The Journal of Wildlife Management 37: 279-287.

Margolis, L., G.W. Esch, J.C. Holmes, A.M. Kuris, and G.A. Schad. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). The Journal of Parasitology 68: 131-133.

Mason, C.F. 1970. Food, feeding rates and assimilation in woodland snails. Oecologia 4: 358-373.

Maze, R.J. and C. Johnstone. 1986. Gastropod intermediate hosts of the meningeal worm *Parelaphostrongylus tenuis* in Pennsylvania: observations on their ecology. Canadian Journal of Zoology 64: 185-188.

Michigan Department of Natural Resources (MDNR). 1996. 1938-1996 Michigan deer population figures. Unpublished. 1 pp.

-------- 1997. Result of moose census. Unpublished memo. 5 pp.

Moore, A.M. 1986. Temperature and moisture dependence of decomposition rates of hardwood and coniferous leaf litter. Soil Biology and Biochemistry 18: 427-435.

Newcomb, L. 1977. Newcomb's wildflower guide. Little, Brown and Company, Boston, Massachusettes. 490 pp.

Pitt, W.C. and P.A. Jordan. 1994. A survey of the nematode parasite, *Parelaphostrongylus tenuis* in the white-tailed deer, *Odocoileus virginianus*, in a region proposed for caribou, *Rangifer tarandus caribou*, re-introduction in Minnesota. The Canadian Field-Naturalist 108: 341-346.

Platt, T.R. 1978. The lifecycle and systematics of Parelaphostrongylus odocoilei (Nematoda: Metastrongyloidea), a parasite of mule deer (Odocoileus hemionus hemionus), with special reference to the molluscan intermediate host . Ph.D. thesis, Department of Zoology, University of Alberta, Edmonton, Alberta. 233 pp.

Platt, T.R. 1989. Gastropod intermediate hosts of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) from northwestern Indiana. The Journal of Parasitology 75:519--523.

Prior, D.J. 1985. Water-regulatory behaviour in terrestrial gastropods. Biological Research 60: 403-424.

Raskevitz, R.F., A.A. Kocan, and J.H. Shaw. 1991. Gastropod availability and habitat utilization by wapiti and white-tailed deer sympatric on range enzootic for meningeal worm. Journal of Wildlife Diseases 27: 92-101.

Renecker, L.A. 1987. Bioenergetics and behavior of moose (Alces alces) in the apsen dominated boreal forest. Ph.D. thesis, Department of Animal Science, University of Alberta, Edmonton, Alberta. 265 pp.

Renecker, L.A. and R.J. Hudson. 1986. Seasonal foraging rates of free-ranging moose. The Journal of Wildlife Management 50: 143 - 47.

Renecker, L.A. and C.C. Schwartz. 1997. Food habits and feeding behavior. Pages 403-439 *In* A.W. Franzmann and C.C. Schwartz (eds.), Ecology and management of the North American moose. Smithsonian Institution Press, Washington D.C. 733 pp.

Ritcey, R.W. and N.A.M. Verbeek. 1969. Observations of moose feeding on aquatics in Bowron Lake Park, British Columbia. The Canadian Field-Naturalist 83: 339-343.

Robb, L.A. 1987. Gastropod intermediate hosts of lungworms (Nematoda: Protostrongylidae) on a bighorn sheep winter range: aspects of transmission. M.Sc. thesis, Department of Zoology, University of Alberta, Edmonton, Alberta. 111 pp.

Robb, L.A., and W.M. Samuel. 1990. Gastropod intermediate hosts of lungworms (Nematoda: Protostrongylidae) on bighorn sheep winter range: aspects of transmission. Canadian Journal of Zoology 68: 1976-1982.

Rowley, M.A., E.S. Loker, J.F. Pagels, and R.J. Montali. 1987. Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National Zoological Park's Conservation and Research Center, Virginia. The Journal of Parasitology 73: 1084-1089.

Samuel, W.M., T.R. Platt, and S.M. Knispel-Krause. 1985. Gastropod intermediate hosts and transmission of *Parelaphostrongylus odocoilei*, a muscle-inhabiting nematode of mule deer, *Odocoileus h. hemionus*, in Jasper National Park, Alberta. Canadian Journal of Zoology 63: 928-932.

Schwartz, C.C. 1992. Techniques of moose husbandry. Supplement to Alces 1: 177-192.

Schwartz, C.C., W.L. Regelin, and A.W. Franzmann. 1984. Seasonal dynamics of food intake in moose. Alces 20: 223-244.

Shostak, A.W. and W.M. Samuel. 1984. Moisture and temperature effects on survival and infectivity of first-stage larvae of *Parelaphostrongylus odocoilei* and *P. tenuis* (Nematoda: Metastrongyloidea). The Journal of Parasitology 70: 261-269.

Skinner, W.R. and E.S. Telfer. 1974. Spring, summer, and fall foods of deer in New Brunswick. The Journal of Wildlife Management 38: 210-214.

Strandine, E.J. 1941. Quantitative study of a snail population. Ecology 22: 86-91.

Strayer, D., D.H. Pletscher, S.P. Hamburg, and S.C. Nodvin. 1986. The effects of forest disturbance on land gastropod communities in northern New England. Canadian Journal of Zoology 64: 2094-2098.

ter Braak, C.J.F. 1987a. CANOCO - a FORTRAN program for canonical community ordination by partial, detrended, canonical correspondence analysis, principal components analysis, and redundancy analysis (version 2.1). TNO Institute of Applied Computer Sciences, Wageningen, Netherlands. 92 pp.

-------- 1987b. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetation 69: 69-77.

Upshall, S.M., M.D.B. Burt, and T.G. Dilworth. 1986. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in terrestrial gastropods. Journal of Wildlife Diseases 22: 582-585.

Van Deelen, T.R., K.S. Pregitzer, and J.B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. The American Midland Naturalist 135: 181-194.

Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan. Journal of Forestry 63: 523-529.

Voss, E.G. 1972. Michigan Flora, Part I Gymnosperms and Monocots. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 488 pp.

-------- 1985. Michigan Flora, Part II Dicots (Saururaceae - Cornaceae). Regents of the Universityof Michigan, Ann Arbor, Michigan. 724 pp.

Walton, M.L. 1963. Length of life in west American land snails. The Nautilus 76: 127-131.

Weckerly, F.W. and M.L. Kennedy. 1992. Examining hypotheses about feeding strategies of white-tailed deer. Canadian Journal of Zoology 70: 432-439.

Whitlaw, H.A., M.W. Lankester, and W.B. Ballard. 1996. _Parelaphostrongylus_ _tenuis_ in terrestrial gastropods from white-tailed deer winter and summer range in northern New Brunswick. Alces 32: 75-83.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey. 718 pp.

Personal Communications

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CHAPTER IV. GENERAL CONCLUSION

This study examined the current population size of *P. tenuis* in white-tailed deer (WTD) and the ecology of gastropod intermediate hosts in Michigan's upper peninsula. Results offer a better understanding of potential risks for the area's recently reintroduced moose population. Six major hypotheses were tested and the results were as follows:

> **Ho1**: Population size of adult *P. tenuis* is similar among deer of different geographic location, age, and gender within Michigan's upper peninsula, **Ha1**: Population size of adult *P. tenuis* varies between location, age, and gender within Michigan's upper peninsula.
>
>> Prevalence did not differ between locations within the western portion of the upper peninsula, nor did it differ between host gender. Prevalence differed by host age being much lower in fawns than yearlings or adults.
>
> **Ho2**: Shedding of first-stage larvae in feces of WTD does not differ by month throughout the year, and **Ha2**: Shedding of first-stage larvae in feces of WTD fluctuates seasonally in accord with findings for other related nematodes.
>
>> Results were consistent with previous published reports on *P. tenuis* and related nematodes; numbers of larvae increased gradually through winter and peaked in early spring.
>
> **Ho3**: Meningeal worm is the only protostrogylid nematode in WTD and gastropods of Michigan's upper peninsula, **Ha3**: Other related worms such as *P. andersoni* and *Varestrongylus alpenae* occur in WTD and gastropods of Michigan's upper peninsula.
>
>> Results were inconclusive regarding presence of these parasites, because although both have been reported previously from WTD in Michigan's upper peninsula, neither parasite was found in the current study. The fact remains that one or both parasites are most likely present in WTD of the upper peninsula. Evidence from the literature, plus indirect evidence from the current study (presence of short L1s in feces of WTD that were within the size range for *V. alpenae*), strengthen this argument. However, based on many published accounts of high prevalence of *P. tenuis* in the midwest region, and the fact that few concurrent infections have been found in naturally infected

deer, *P. tenuis* is probably the most prevalent protostrongylid parasite in WTD of Michigan's upper peninsula.

Ho4: Densities of gastropods will be random across varying habitats and disturbed areas, **Ha4**: Densities of gastropods will vary greatly according to habitat and human disturbance.

Results suggest that gastropods were more abundant in lowland areas, although of various habitats. Gastropods were also very abundant in recently logged deer yards (*i.e.*, site 415 in 1995 and site 410 in 1996). Disturbance probably contributed to the large numbers of gastropods at some of these sites, but another factor may be concentrations of WTD feces that increased organic nutrients in the soil.

Ho5: Many species of gastropods will be infected naturally with *P. tenuis*, **Ha5**: Few species of gastropods will be infected naturally with *P. tenuis* larvae.

As predicted, only eight species of gastropods were infected and no new species of intermediate host was identified. Many of the important intermediate host species were widely distributed which has important implications for transmission of *P. tenuis* in Michigan.

Ho6: Infected gastropods will be randomly distributed throughout areas inhabited by deer or moose. **Ha6**: Densities of infected gastropods will vary greatly between areas inhabited by deer or moose.

Results suggest that focal areas of gastropods infected with *P. tenuis* exist in the upper peninsula. Evidence for deer yards as foci was present in both 1995 and 1996, particularly for certain deer yards (*e.g.* site 415 in 1995 and site 404 in 1996). Considering the huge numbers of larvae deposited by WTD and the abundance of potential intermediate hosts in such areas, numbers of infected gastropods were not as numerous as predicted.

The primary moose range (see Figure 1-3), where a majority of the total 120 moose were found during the survey of 1997 (Rob Aho, personal communication), has a highland area and a lowland area that includes a network of lakes, streams and swamps. Deer concentrate in lowland areas along the edge of Lake Superior in winter and disperse widely in summer.

Throughout the year, deer densities in the primary moose range are lower than surrounding areas probably because forests are older there. Although no area in the upper peninsula is completely devoid of WTD, moose that remain in the primary range probably overlap relatively little with WTD compared to moose that venture outside the apparent perimeter. Spatial separation between deer and moose suggests that potential foci of infected gastropods, in the form of deer yards, are not critical areas for transmission of *P. tenuis* to moose that remain within the primary range.

Deer yards as foci probably contribute more to transmission of *P. tenuis* between resident WTD than between deer and sympatric moose, and even for WTD such contribution may be minor. Only relatively low densities of WTD that live all year along the edge of Lake Superior have access to these potential foci during snow-free seasons. Also, based on intensities of infection from different age classes of WTD in this study and in many published studies, it appears that deer eventually become resistant to reinfection with *P. tenuis* (see Lankester and Samuel 1997).

Intuitively, all deer yards should potentially serve as foci for transmission because deer deposit large amounts of contaminated feces in localized areas and potential intermediate hosts are present in all habitat types. However, the degree of infectivity of a deer yard depends on a combination of interacting factors (Figure 4-1), which include: 1) environmental conditions: habitat type, soil type, and variations in climate; 2) biotic factors: numbers and species of gastropods and numbers of deer; and 3) human influences: logging or artificial feeding of deer that affect distribution of definitive hosts and probably gastropods. Because these factors are dynamic and interactive, they affect deer yards as foci for potential transmission of *P. tenuis* in numerous ways. Regardless where deer congregate there are multiple factors affecting transmission of L1s to gastropod intermediate hosts. Additional factors surrounding specific habitat use by moose and deer influence the timing and rate of which infected gastropods will be ingested by definitive hosts if they do visit such areas during snow-free seasons. This suggests that deer yards may not create as many "hot spots" for transmission as some researchers have anticipated.

Transmission probably occurs most often at random and low-levels. Deer often disperse from yards in March unless winters are severe, therefore, L1s shed by WTD become widely distributed. Anderson and Prestwood (1981) suggested that deer will eventually become infected, even with low densities of infected gastropods, because of the large amounts of food they consume. Deer not only consume large quantities of vegetation but much of it is at ground level (Skinner and Telfer 1974). Deer probably acquire infections during any snow-free season, whereas moose may be most vulnerable during autumn when feeding habits include more ground-level vegetation.

Growth of Michigan's moose population has been slow. Current estimated numbers of moose equal numbers predicted for 1989 only 4 yrs after the initial translocation. Questions remain as to why offspring remain unaccounted for despite apparently stable reproductive rates of female moose in the primary range (Aho 1995).

Overall, young moose may be more vulnerable to infections with *P. tenuis* than older moose. Young moose are probably more susceptible to ingesting infected gastropods in summer and early fall because of the progressive feeding on vegetation as they become weaned. Also, dispersal of young moose outside the primary range may increase the likelihood of encountering habitats with higher densities of deer. Higher deer densities are often associated with agricultural land and large-scale forest management practices such as clear-cutting. Although scattered, both land use practices surround the primary moose range. Moose that wander through these areas with higher deer densities have higher potential for encountering infected gastropods because important intermediate hosts are widely distributed. The risk of acquiring infection would be even greater if moose that left the primary range, migrated back for winter, thereby passing through potentially contaminated areas during both spring and autumn.

Although the role of *P. tenuis* in limiting sympatric populations of moose is not fully understood, it is a fact that meningeal worm alone caused one-third of diagnosed deaths in the upper peninsula since the translocation. Taking into account other mortality-causing factors such as predation and other parasites or disease, *P. tenuis* has high potential to complicate an already challenging situation for a recently established moose population struggling to increase in numbers and range.

Management Implications

Now that we have some idea of numbers of terrestrial gastropods and their habitat preferences in Michigan's upper peninsula, a thorough survey of resources utilized by moose in the primary range is warranted. Studies of specific habitat-use patterns of moose, particularly examining the overlap with wide-ranging WTD, would offer insight as to where and when moose acquire deadly parasites because this study has determined that potential intermediate hosts are just about everywhere. The range of moose does not appear to be growing very steadily. Primary range remains a small island of isolated habitat that offers adequate winter habitat in close proximity to adequate summer habitat and yet separated from high densities of deer. The safest corridors for dispersing moose searching for new territories would be areas of low deer use to ensure lowest possible exposure to meningeal worm and other parasites.

Maintenance of deer populations at or below 5 deer/km^2 through liberal hunting regulations would decrease contamination of habitats with *P. tenuis* larvae. The deer population in the upper peninsula grew to record numbers between 1988 and 1995 (see Chapter I, pages 8-10). Such numbers potentially harm moose in two ways, through direct competition for resources and indirectly through mortality caused by parasites of WTD. In fact, deer in the upper peninsula harbor two parasites, *P. tenuis* and the giant liver fluke, *Fascioloides magna*, the latter of which causes severe necrosis of the liver in moose (Lankester 1974). Both parasites do little harm to deer but can be fatal for moose. Combined, these two parasites caused 48% of the diagnosed deaths ($n = 43$) between 1985 and 1994 (Aho 1995). Keeping deer numbers low will decrease the potential for parasite-induced mortality of moose. Monitoring of lethal parasites (*i.e., P. tenuis* and *Fascioloides magna*) in the WTD population would keep managers informed of potential changes in mortality of moose caused by disease and/or predation of diseased animals.

Spatial separation between winter deer yards and primary moose habitat ensure that deer yards as foci of infected gastropods will not act as primary sites for transmission of *P. tenuis* to moose. Therefore, this spatial separation should be maintained. Winter logging in primary moose range should be discouraged until late December or early January after deer have passed through the area to lower elevations along Lake Superior. If logging occurs before late December, it might attract and hold WTD within primary moose range during times when deer are depositing the greatest numbers of meningeal worm larvae in their feces. Inevitably clear-cut logging is a part of the upper peninsula environment, but let us be clear that such cutting practices will be attractive for WTD and nearly half those deer will be infected with *P. tenuis*. Therefore, the more clear-cuts done within the primary range for moose, the more cases of *P. tenuis* induced neurological disease will occur.

Unfortunately any forest management practice that creates openings has potential to bring moose and deer into close proximity with each other, therefore specific management options are limited. Treatment of wild ungulates with anti-helminthic drugs is expensive, difficult to administer, and a temporary solution. Controlling terrestrial gastropod numbers is ecologically unsound and probably impossible to do over large areas. The feasible options include: 1) protect primary moose range from large-scale habitat manipulation and high deer densities, 2) identify habitat that is similar to the current primary moose range and create or protect potential corridors for moose to reach these areas, 3) keep deer densities low in areas that surround primary moose range thereby decreasing potential risk for moose to acquire deadly parasites when they leave the primary range, and 4) continually monitor changes in parasite population sizes of meningeal worm and liver fluke in WTD. A monitoring program will assist in making appropriate management decisions for moose.

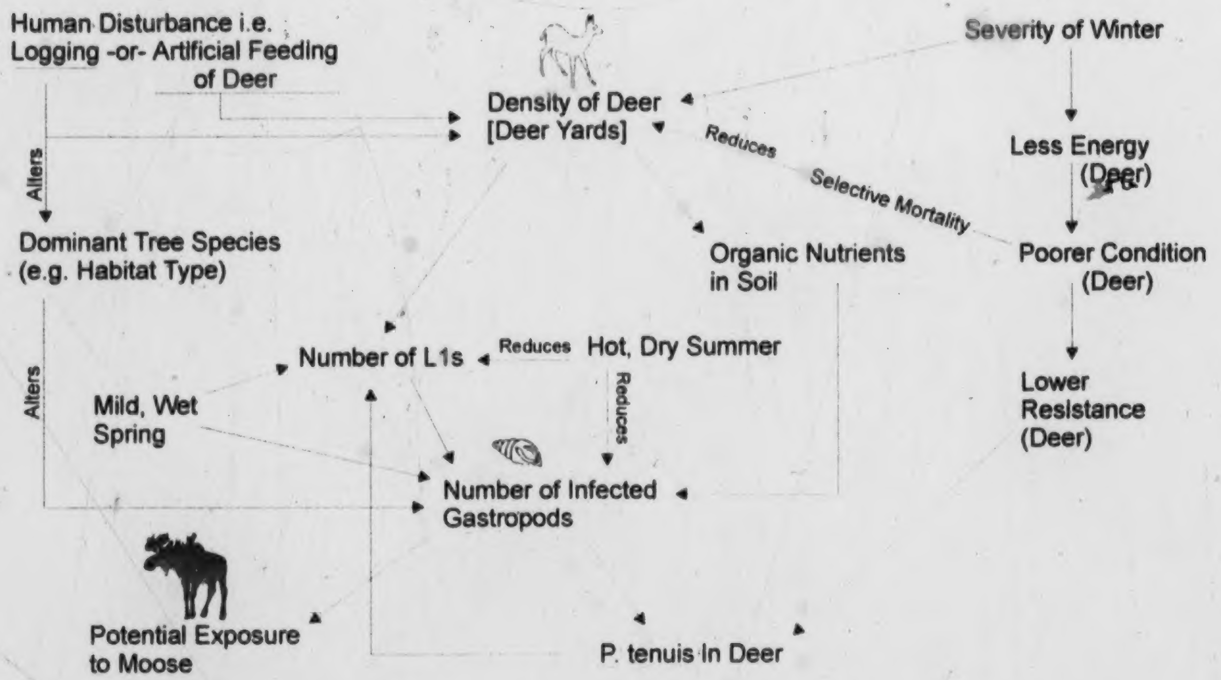
Human Disturbance i.e. Logging -or- Artificial Feeding of Deer
Density of Deer [Deer Yards]
Severity of Winter
Altered
Reduces
Selective Mortality
Less Energy (Deer)
Dominant Tree Species (e.g. Habitat Type)
Organic Nutrients in Soil
Poorer Condition (Deer)
Number of L1s
Reduces
Hot, Dry Summer
Altered
Mild, Wet Spring
Reduces
Lower Resistance (Deer)
Number of Infected Gastropods
Potential Exposure to Moose
P. tenuis In Deer

Figure 4-1. Model of factors that influence deer yards as foci for transmission of *Parelaphostrongylus tenuis*. All arrows indicate an increase unless stated otherwise.

Literature Cited

Aho, R.W. 1995. Michigan's translocated moose population: 10 years later. Michigan Department of Natural Resources Wildlife Division Report Number 3245. 18 pp.

Anderson, R. C. and A. K. Prestwood. 1981. Lungworms. Pages 266 - 317 *In* Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.), Diseases and parasites of white-tailed deer. Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida. 458 pp.

Lankester, M.W. 1974. *Parelaphostrongylus tenuis* (Nematoda) and *Fascioloides magna* (Trematoda) in moose of southeastern Manitoba. Canadian Journal of Zoology 52: 235-239.

Lankester, M.W. and W.M. Samuel. 1997. Pests, parasites and diseases. Pages 479-517 *In* C.C. Schwartz and A.W. Frazmann (eds.), Ecology and Management of the North American Moose. A Wildlife Management Institute Book, Smithsonian Institution Press, Washington D.C. 733 pp.

Skinner, W.R. and E.S. Telfer. 1974. Spring, summer, and fall foods of deer in New Brunswick. The Journal of Wildlife Management 38: 210-214.

Personal Communications

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Appendix Ia. Descriptions of gastropod collection sites, 1995.

Site Number*	Legal Description	% Conifer Component	Mean % Canopy Cover	Habitat** Category
104 - H	T.51N.-R.33W.-Section 04	36	60	1
109 - D	T.52N.-R.33W.-Section 09	67	60	1
120 - H	T.51N.-R.33W.-Section 20	0	70	3
209 - H	T.50N.-R.33W.-Section 09	0	80	3
212 - D	T.50N.-R.34W.-Section 12	36	60	1
216 - H	T.50N.-R.32W.-Section 16	70	70	2
217 - H	T.50N.-R.33W.-Section 17	0	80	3
225 - H	T.50N.-R.33W.-Section 25	48	70	1
305 - H	T.48N.-R.32W.-Section 05	0	0	4
318 - M	T.48N.-R.32W.-Section 18	84	70	2
321 - M	T.47N.-R.33W.-Section 21	55	70	1
324 - M	T.48N.-R.32W.-Section 24	85	60	2
330 - M	T.48N.-R.33W.-Section 30	6	80	3
413 - H	T.51N.-R.31W.-Section 13	33	90	1
415 - D	T.51N.-R.31W.-Section 15	66	90	1
424 - D	T.51N.-R.32W.-Section 24	79	30	2
432 - H	T.52N.-R.30W.-Section 32	0	60	3
436 - H	T.52N.-R.30W.-Section 36	0	80	3
531 - D	T.49N.-R.33W.-Section 31	3	60	3
631 - D	T.49N.-R.33W.-Section 31	0	0	4
532 - D	T.50N.-R.33W.-Section 32	20	60	3
632 - D	T.50N.-R.33W.-Section 32	0	0	4

* D = Deer Congregation Areas, M = Moose Inhabited Areas, H = Miscellaneous Areas

** Habitat categories: 1 = Mixed Conifer and Deciduous, 2 = Predominately Conifer (≥ 70%), 3 = Predominately Deciduous (≥ 70%), 4 = Grass

Appendix Ib. Descriptions of gastropod collection sites, 1995.

Reference Number*	Depth of Watertable**	Mean Depth of Top Soil (cm)	Permeability Category+	Type of Top Soil++
104 - H	5	6.6	2	Red/Brown Sandy Loam
109 - D	2	7.8	2	Black Loamy Sand
120 - H	3	2.0	2	Black Loamy Sand
209 - H	3	2.3	2	Black Loamy Sand
212 - D	1	1.4	1	Dark Brown Muck
216 - H	3	1.5	2	Black Loamy Sand
217 - H	3	1.9	3	Black Loamy Sand
225 - H	2	9.5	2	Litter Covered Loamy Sand
305 - H	1	5.4	1	Dark Brown Muck
318 - M	1	2.1	1	Dark Brown Muck
321 - M	2	6.1	2	Litter Covered Loamy Sand
324 - M	5	10.6	2	Litter Covered Loamy Sand
330 - M	3	11.8	2	Litter Covered Loamy Sand
413 - H	3	6.5	3	Black Loamy Sand
415 - D	2	10.2	3	Litter Covered Mottled Sand
424 - D	5	4.0	3	Litter Covered Mottled Sand
432 - H	3	3.2	2	Black Loamy Sand
436 - H	2	2.4	2	Black Loamy Sand
531 - D	2	4.1	2	Litter Covered Silt Loam
631 - D	4	1.9	1	Silt Loam
532 - D	3	12.7	3	Black Loamy Sand
632 - D	2	2.1	3	Black Loamy Sand

*D = Deer Congregation Areas, M = Moose Inhabited Areas, H = Miscellaneous Areas
** Depth of watertable interpreted from Berndt (1988): 1 = perched < 0.2 m, 2 = 0.2 - 0.5 m, 3 = 0.51 - 0.75 m, 4 = 0.76 - 1 m, 5 = > 1m + Rate of permeability interpreted from Berndt (1988): 1 = Slow (< 1 cm/hr), 2 = Moderate (1.1 - 5 cm/hr), 3 = Rapid (>5 cm/hr) ++ Types of top soil from Berndt (1988)

Appendix Ic. Descriptions of gastropod collection sites, 1995.

Site Number*	Approximate Number of Deer**	Miscellaneous Notations
104 - H	----	None
109 - D	25 < 50	Deer artificially fed during winter within 600 m, also nearby open field within 400 m, deer trails throughout.
120 - H	----	Open field within 500 m.
209 - H	----	Dry upland area in a new subdivision.
212 - D	50 < 100	Mucky soil, annual deer yard, resting area between artificial feed sites.
216 - H	----	White spruce stand surrounded by a large maple stand.
217 - H	----	None
225 - H	----	None
305 - H	----	Young trees scattered, mainly open grass, wet with pooling water.
318 - M	----	Moose tracks on site, browse sign within 500 m, wetland within 1 km.
321 - M	----	Moose tracks, wetland within 1 km.
324 - M	----	Moose tracks, wetland within 1 km.
330 - M	----	Moose tracks, browse sign within 300 m, wetland within 1 km.
413 - H	----	None
415 - D	50 < 100	Deer trails, recently logged area within 500 m.
424 - D	50 < 100	Deer artificially fed during winter, red pine plantation.
432 - H	----	Youngest stand and most disturbed, old skid trail.
436 - H	----	Wild apple patch within 100 m.
531 - D	< 25	Deer beds present, deer trails.
631 - D	< 25	Roadside ditch, grass, pooling water within 1 m.
532 - D	< 25	Deer beds present, deer trails.
632 - D	< 25	Roadside ditch, grass, pooling water within 1 m.

*D = Deer Congregation Areas, M = Moose Inhabited Areas, H = Miscellaneous Areas

** Approximate numbers of deer that congregated at the sites according to observations by people who fed them, by relative density of pellet groups along trails, and by personal observation.

Appendix IIa. Description of gastropod collection sites, 1996.

Site Number*	Legal Description	% Conifer Component	Mean % Canopy Cover	Habitat** Category
212 - DR	T.50N.-R.34W.-Section 12	34	60	1
225 - R	T.50N.-R.33W.-Section 25	47	80	1
302 - M	T.48N.-R.33W.-Section 02	30	80	3
307 - M	T.48N.-R.32W.-Section 07	55	60	1
309 - M	T.48N.-R.32W.-Section 09	80	50	2
311 - M	T.48N.-R.32W.-Section 11	90	60	2
401 - D	T.51N.-R.31W.-Section 01	30	60	3
404 - D	T.51N.-R.31W.-Section 04	14	70	3
406 - D	T.51N.-R.30W.-Section 06	74	90	2
410 - D	T.51N.-R.30W.-Section 10	52	70	1
423 - D	T.51N.-R.32W.-Section 23	70	80	2
631 - R	T.49N.-R.33W.-Section 31	None	0	4
632 - R	T.50N.-R.33W.-Section 32	None	0	4

* D = Deer congregation Area, M = Moose Inhabited Area, R = Repeat Collection Area

** Habitat categories: 1 = Mixed Coniferand Decidous, 2 = Predominantly Conifer (≥70%), 3 = Predominantly Decidous (≥70%), 4 = Grass

Appendix IIb. Description of gastropod collection sites, 1996.

Site Number*	Depth of Watertable**	Mean Depth of Top Soil (cm)	Permeability Catergory⁺	Type of Top Soil ⁺⁺
212 - DR	1	1.4	1	Dark Brown Muck
225 - R	2	9.5	2	Litter Covered Loamy Sand
302 - M	1	3.3	2	Silt Loam
307 - M	3	2.6	2	Litter Covered Silt Loam
309 - M	1	3.9	1	Dark Brown Muck
311 - M	2	1.5	2	Black Sandy Loam
401 - D	3	6.6	2	Black Loamy Sand
404 - D	3	4.1	2	Black Loamy Sand
406 - D	3	10.2	3	Litter Covered Loamy Sand
410 - D	2	10.8	3	Litter Covered Loamy Sand
423 - D	2	2.6	3	Red/Brown Sandy Loam
631 - R	4	1.9	1	Silt Loam
632 - R	2	2.1	3	Black Loamy Sand

* D = Deer congregation area, M = Moose inhabited area, R - Repeat collection area from 1995

** Approximate depth of watertable interpreted from Berndt (1988): 1 = perched (< 0.2 m), 2 = 0.2 - 0.5 m, 3 = 0.51 - 0.75 m, 4 = 0.76 - 1 m, 5 = > 1 m.

⁺ Rate of permeability interpreted from Berndt (1988): 1 = Slow (< 1 cm/hr), 2 = Moderate (1 - 5 cm/hr), 3 = Rapid (> 5 cm/hr)

⁺⁺ Types of top soil after Berndt (1988)

Appendix IIc. Descriptions of gastropod collection sites, 1996.

Site Number*	Approximate** Numbers of Deer	Miscellaneous Notations
212 - DR	< 50	Mucky soil, deer yard in winter. Fewer deer in 1996 than in 1995.
225 - R	-----	None
302 - M	-----	Moose tracks, moose sighted in spring.
307- M	-----	Moose tracks present in spring, wetland within 800 m.
309 - M	-----	Moose tracks, browse signs, cow and calf sighted in summer, wetland within 0.5 km.
311 - M	-----	Moose tracks, wetland within 1 km.
401 - D	< 50	Deer were artificially fed on site throughout winter.
404 - D	≥ 200	Logging within 1 km, deer artificially fed on site throughout winter.
406 - D	50 < 100	Winter bedding area, artificially fed within 3 km.
410 - D	100 < 200	Logged throughout winter, both bedding and feeding area.
423 - D	50 < 100	Winter bedding area, artificially fed within 1 km.
631 – R	-----	Roadside ditch used by deer in spring and summer 1995. Deer were rarely seen here during 1996.
632 - R	-----	Roadside ditch used for spring and summer feeding in 1995. Deer were rarely seen here during 1996.

* D = Deer concentration areas, M = Moose inhabited areas, R = Repeat collection areas from 1995

** Approximate numbers of deer estimated according to people them and personal observations.

Appendix III. Prevalence and intensity of infected gastropods by site in 1995.

Site*	Total Collected	Number Infected	Percent Prevalence	Mean Intensity
104-H	479	3	0.6	1
109-D	680	2	0.3	1
120-H	197	1	0.5	1
209-H	219	1	0.5	1
212-D	868	4	0.5	2.75
216-H	217	0	0	0
225-H	223	1	0.5	1
305-H	141	0	0	0
318-M	113	0	0	0
321-M	277	0	0	0
324-M	382	1	0.3	1
330-M	173	3	1.7	1.33
413-H	300	0	0	0
415-D	504	5	1.0	1
424-D	49	1	2.0	1
432-H	278	1	0.4	1
436-H	83	0	0	0
531-D	70	4	5.7	1.25
631-D	312	2	0.6	1
532-D	149	1	0.7	3
632-D	154	0	0	0
Total	5880	30	0.5	1.4

*D = Areas Where Deer Congregated, M= Areas Where Moose Inhabited,
H = Miscellaneous Areas.

Appendix IV. Prevalence and intensity of infected gastropods by site in 1996.

Site*	Total Collected	Total Infected	Percent Prevalence	Mean Intensity
212-DR	571	1	0.2	8.0
225-R	171	0	0	0
302-M	209	2	1.0	3.0
307-M	160	2	1.3	5.0
309-M	101	0	0	0
311-M	79	1	1.3	1.0
401-D	243	3	1.2	7.7
404-D	347	18	5.2	1.4
406-D	427	3	0.7	1.7
410-D	450	5	1.1	2.6
423-D	185	2	1.1	3.5
631-R	223	0	0	0
632-R	131	1	0.8	11.0
Total	3297	38	1.2	2.9

* D = Areas Where Deer Congregated, M = Areas Where Moose Inhabited, R = Repeat collection sites from 1995

Appendix Va. Total numbers of gastropods per species collected by site in 1995.

	Sites												
Species*	104	109	120	209	212	216	217	225	305	318	321	324	330
ZONARB	205	198	87	108	113	74	6	73	85	24	95	152	10
STREXI	69	105	8	0	2	11	6	29	3	11	49	24	21
DISSPP	125	139	38	16	42	30	17	25	20	38	40	127	79
COLEDE	1	0	0	0	0	0	0	0	0	1	1	1	0
ZOOHAR	1	11	0	0	0	0	0	0	0	0	0	8	12
STRFER	8	3	0	3	0	1	0	5	1	0	4	10	10
STRLAB	5	2	0	1	0	25	0	24	1	0	35	0	0
HELPAR	9	6	12	1	2	1	1	2	0	0	11	7	0
EUCFUL	4	9	1	0	4	5	0	2	1	3	3	6	6
TRIALB	3	0	0	0	0	0	0	0	0	0	1	0	0
CIOLUB	0	54	1	0	499	0	0	0	0	0	0	0	0
STRFRA	0	0	0	0	0	0	0	2	0	0	4	2	0
ANGALT	13	7	39	61	23	1	1	2	0	1	6	1	4
IMMESO	1	0	0	0	0	1	0	7	0	0	0	0	0
DERLAE	23	29	5	24	35	19	16	26	15	25	14	10	14
PALDOR	11	4	3	4	0	2	12	22	6	6	11	32	13
ZONNIT	0	0	0	0	124	0	0	0	0	0	0	0	0
VERTRI	0	39	1	0	0	0	0	0	0	0	0	0	0
DERRET	0	13	0	1	28	0	0	0	10	1	0	0	0
NESELE	0	10	0	0	0	0	0	1	0	0	0	0	0
PUNMIN	2	53	2	0	0	0	0	3	0	3	3	2	8
VITLIM	0	0	0	0	0	0	0	0	1	0	0	0	0
Grand Total	480	682	197	219	872	170	59	223	143	113	277	382	177

* See Appendix VII for abbreviations

Continued

P

Appendix Vb. Total numbers of gastropods per species by site in 1995.

	Sites									
Species*	413	415	424	432	436	531	631	532	632	Grand Total
ZONARB	138	364	2	176	41	13	3	103	41	2111
STREXI	15	17	0	19	17	1	1	0	0	408
DISSPP	14	43	20	3	2	19	21	2	0	860
COLEDE	0	0	0	0	0	0	0	1	0	5
ZOOHAR	0	0	1	3	0	0	0	0	0	36
STRFER	4	3	0	0	1	0	0	0	0	53
STRLAB	25	4	0	2	1	0	0	0	0	125
HELPAR	7	6	0	0	1	0	0	0	0	66
EUCFUL	20	0	1	25	1	0	0	5	0	96
TRIALB	0	3	0	0	0	0	0	0	0	7
CIOLUB	0	0	0	0	0	7	232	0	16	809
STRFRA	0	2	0	0	0	0	0	0	0	10
ANGALT	24	33	0	5	2	1	0	0	1	225
IMMESO	2	2	0	0	1	0	0	1	0	15
DERLAE	2	17	11	8	13	7	8	35	70	426
PALDOR	35	13	13	35	3	0	0	6	1	232
ZONNIT	0	0	0	0	0	0	3	0	25	152
VERTRI	0	0	1	0	0	0	0	0	0	41
DERRET	0	0	0	0	0	23	44	0	0	120
NESELE	0	0	0	1	0	0	0	0	0	12
PUNMIN	14	0	0	1	0	0	0	0	0	91
VALEXC	0	0	0	0	0	0	0	0	0	0
VITLIM	0	0	0	0	0	0	0	0	0	1
	300	507	49	278	83	71	312	153	154	5901

* See Appendix VII for abbreviations

Appendix VI. Numbers of gastropods per species collected by site in 1996.

	Site													
Species*	212	225	302	307	309	311	401	404	406	410	423	631	632	Grand Total
ZONARB	50	82	115	82	22	9	148	277	286	173	34	8	58	1344
STREXI	0	9	12	0	0	0	16	0	10	15	8	0	1	71
DISSPP	57	12	71	9	46	45	54	68	99	195	58	10	2	726
ZOOHAR	0	0	0	0	0	0	0	0	3	0	0	0	0	3
STRFER	0	0	0	0	0	0	0	1	0	6	0	0	0	7
STRLAB	0	23	0	0	0	0	14	0	3	20	51	0	0	111
HELPAR	0	2	4	1	0	1	2	32	0	0	2	0	0	44
EUCFUL	1	2	0	0	0	0	1	0	1	7	2	0	0	14
TRIALB	0	0	0	0	0	0	1	1	1	3	0	0	0	6
CIOLUB	350	0	0	0	0	0	0	0	0	0	0	92	34	476
STRFRA	0	0	0	3	0	0	1	0	2	4	0	0	0	10
ANGALT	23	5	4	32	1	3	11	26	19	17	20	0	0	161
IMMESO	0	4	0	0	0	0	1	1	16	12	0	0	1	35
DERLAE	66	16	10	17	26	18	14	5	10	0	19	23	17	241
PALDOR	1	24	18	30	4	2	17	12	12	0	10	0	1	131
ZONNIT	72	0	0	0	0	0	3	0	0	0	0	0	16	91
VERTRI	0	0	0	0	0	1	0	0	0	0	0	0	0	1
DERRET	6	0	0	0	4	0	0	0	0	0	0	88	5	103
NESELE	0	0	0	0	1	0	13	5	20	0	0	0	3	42
PUNMIN	0	2	1	0	0	0	3	0	0	0	1	0	1	8
VALEXC	0	0	0	0	0	0	0	0	0	0	0	1	6	7
VITLIM	0	0	0	0	1	4	0	0	0	0	0	12	2	19
Grand Total	626	181	235	174	105	83	299	428	482	452	205	234	147	3651

*See Appendix VII for abbreviations.

Appendix VII. Corresponding abbreviations for species collected in northern Michigan in 1995 and 1996.

Species	Abbreviation
Zonitoides arboreus	ZONARB
Striatura exigua	STREXI
Discus spp.*	DISSPP
Columella edentula	COLEDE
Zoogenetes harpa	ZOOHAR
Striatura ferrea	STRFER
Strobilops labrynthica	STRLAB
Helicodiscus parallelus	HELPAR
Euconulus fulvus	EUCFUL
Triodopsis albolabris	TRIALB
Cionella lubrica	CIOLUB
Strenotrema fraternum	STRFRA
Anguispira alternata	ANGALT
Immature Mesodontidae	IMMESO
Deroceras laeve	DERLAE
Pallifera dorsalis	PALDOR
Zonitoides nitidus	ZONNIT
Vertigo tridentata	VERTRI
Deroceras reticulatum	DERRET
Nesovitrea electrina	NESELE
Punctum minitusum	PUNMIN
Vallonia excentrica	VALEXC
Vitrina limpida	VITLIM

**Discus* spp. = *Discus cronkhitei* and *Discus catskillensis*

Appendix VIIIa. Names of plant species identified in 1995 and 1996 with corresponding abbreviations.

Common Name	Species	Abbreviation
Balsam Fir	*Abies balsamea* (L.) Miller	ABIBAL
Red Maple	*Acer rubrum* L.	ACERUB
Sugar Maple	*Acer saccharum* Marsh.	ACESAC
Mountain Maple	*Acer spicatum* Lamar.	ACESPI
Yarrow	*Achillaea millefolium* L.	ACHMIL
Red Top Grass	*Agrostis gigantea* L.	AGRGIG
Speckled Alder	*Alnus rugosa* (Du Roi) Spren.	ALNRUG
Sarsasparilla	*Aralia nudicaulis* L.	ARANUD
Jack in the Pulpit	*Arisaema atrorubens* (Ait.) Blume	ARISPP
Stiff Aster	*Aster linariifolius* L.	ASTLIN
Large Leaf Aster	*Aster macrophyllus* L.	ASTMAC
Black Aster	*Aster spp.*	ASTSPP
Lady Fern	*Athyrium felix femina* L.	ATHFEL
Yellow Birch	*Betula alleghaniensis* Britt.	BETALL
White Birch	*Betula paperifera* Marsh.	BETPAP
Oxeye Daisy	*Chrysanthemum leucanthemum* L.	CHRLEU
Water Hemlock	*Cicuta maculata* L.	CICMAC
Blue Beadlily	*Clintonia borealis* (Ait.) Raf.	CLIBOR
Gold Thread	*Coptis groenlandiea* Oeder	COPGRO
Bunch Berry	*Cornus canadensis* L.	CORCAN
Beaked Hazelnut	*Corylus cornuta* Marsh.	CORCOR
Orchard Grass	*Dactylus glomerata* L.	DACGLO
Queen Annes Lace	*Daucus carota* L.	DANCAR
Bush Honeysuckle	*Diervilla lonicera* Mill.	DIELON
Oak Fern	*Dryopteris disjuncta* (Ledeb) C.V. Mort.	DRYDIS
Long Beech Fern	*Dryopteris phegopteris* (L.) Christens.	DRYPHE
Shield Fern	*Dryopteris spinulosa* (O.F. Mull.)	DRYSPI
Quack Grass	*Elytrigia repens* L.	ELYREP
Trailing Arbutus	*Epigaea repens* L.	EPIREP
Marsh Horsetail	*Equisetum palustra* L.	EQUPAL
Wood Horsetail	*Equisetum sylvaticum* L.	EQUSYL
Wild Strawberry	*Fragaria virginiana* Mill.	FRAVIR
White Ash	*Fraxinus americanus* L.	FRAAME
Black Ash	*Fraxinus nigra* Marsh.	FRANIG
Winter Green	*Gaultheria procumbens* L.	GAUPRO
Rattlesnake Plantain	*Goodyera tesselata* Lodd.	GOOTES
Orange Hawkweed	*Hieracium aurantiacum* L.	HIEAUR
Wild Iris	*Iris versicolor* L.	IRIVER
Tamarack	*Larix laricina* (Du Roi) K. Koch	LARLAR
Fly Honeysuckle	*Lonicera canadensis* Marsh.	LONCAN

Continued

Appendix VIIIb. Names of plant species identified in 1995 and 1996 with corresponding abbreviations.

Common Name	Species	Abbreviation
Stiff Clubmoss	*Lycopodium annotinum* L.	LYCANN
Shiny Clubmoss	*Lycopodium lucidulum* L.	LYCLUC
Ground Pine	*Seliginella selaginoides* L.	LYCSPP
Northern white bugleweed	*Lycopus uniflorus* Michx.	LYCUNI
Lily of Valley	*Maianthemum canadense* Desf.	MAICAN
Wild Apple	*Malus sylvestrus* Mill.	MALSYL
Ostrich Fern	*Matteuccia struthiopteris* (Willd.)	MATSTR
Partridge Berry	*Mitchella repens* L.	MITREP
sensitive fern	*Onoclea sensibilis* L.	ONOSEN
Sweet Cicely	*Osmorhiza daytoni* (Michx.) C.B. Clarke	OSMDAY
Cinnamon Fern	*Osmunda cinnamonea* L.	OSMCIN
Interupted Fern	*Osmunda claytoniana* L.	OSMCLA
Iron Wood	*Ostrya virginiana* (Mill.) K. Koch	OSTVIR
Creeping Wood Sorrel	*Oxalis corniculata* L.	OXACOR
Common Wood Sorrel	*Oxalis montana* Raf.	OXAMON
Sweet Coltsfoot	*Petasites palmatus* Ait.	PETPAL
Timothy Grass	*Phleum pratense* L.	PHLPRA
White Spruce	*Picea glauca* (Moench) A. Voss	PICGLA
Black Spruce	*Picea mariana* (Mill.)	PICMAR
Red Pine	*Pinus resinosa* Ait.	PINRES
White Pine	*Pinus strobus* L.	PINSTR
Common Plantain	*Plantago major* L.	PLAMAJ
Hairy Solomon Seal	*Polygonatum pubescens* (Willd.) Pursh	POLPUB
Polytrichium	*Polytrichium spp.*	POLSPP
Trembling Aspen	*Populus tremuloides* Michx.	POPTRE
Pin Cherry	*Prunus pensylvanica* L.	PRUPEN
Black Cherry	*Prunus serotina* Ehrhart	PRUSER
Bracken Fern	*Pteridum aquilinum* L.	PTEAQU
Choke Cherry	*Pyrus arbutifolia* L.	PYRARB
Raspberry	*Rubus idaeus* L.	RUBIDAE
Thimble Berry	*Rubus parviflorus* Nutt.	RUBPAR
Common Elderberry	*Sambucus canadensis* L.	SAMCAN
Mad-dog Skull Cap	*Scutellaria lateriflora* L.	SCULAT
False Solomon Seal	*Smilacina racemosa* (L.) Desf.	SMIRAC
Golden Rod	*Solidago rugosa* Mill.	SOLSPP
Twisted Stalk	*Streptopus amplexifolius* (L.) D.C.	STRAMP

Continued

Appendix VIIIc. Names of plant species identified in 1995 and 1996 with corresponding abbreviations.

Common Name	Species	Abbreviation
White Cedar	*Thuja occidentalis* L.	THUOCC
Bass Wood	*Tilia americana* L.	TILAME
Star Flower	*Trientalis borealis* Raf.	TRIBOR
Common White Clover	*Trifolium repens* L.	TRIREP
Large Flowered Trillium	*Trillium grandiflorum* (Michx.) Salisb.	TRIGRA
Eastern Hemlock	*Tsuga canadensis* (L.) Carr.	TSUCAN
Late Sweet Blueberry	*Vaccinium angustifolium* Ait.	VACANG
Canada Blueberry	*Vaccinium myrtilloides* Michx.	VACMYR
Bog Bilberry	*Vaccinium uliginosum* L.	VACULI
Maple Viburnum	*Viburnum acerifolium* L.	VIBACE
Canada White Violet	*Viola canadensis* L.	VIOCAN
Early Blue Violet	*Viola palmata* L.	VIOPAL
Smooth Yellow Violet	*Viola pensylvanica* Michx.	VIOPEN
Downy Yellow Violet	*Viola pubescens* Ait.	VIOPUB
Misc Grass		MISGRS
Misc Sedge		MISSDG
Moss		MISMOS
Balsam Seedling	*Abies balsamea* (L.) Mill.	ABISDL
Red Maple Seeding	*Acer rubrum* L.	ARUSDL
Sugar Maple Seedling	*Acer saccharum* Marsh.	ACESDL
Alder Seedling	*Alnus rugosa* (Du Roi) Spren.	ALNSDL
Yellow Birch Seedling	*Betula alleghaniensis* Britt.	BALSDL
White Birch Seedling	*Betula paperifera* Marsh.	BETSDL
Hazelnut Seedling	*Corylus cornuta* Marsh.	CORSDL
White Ash Seedling	*Fraxinus americanus* L.	FAMSDL
Black Ash Seedling	*Fraxinus nigra* Marsh.	FRASDL
Ironwood Seedling	*Ostrya virginiana* (Mill.) K. Koch	OSTSDL
Aspen Seedling	*Populus tremuloides* Michx.	POPSDL
Cherry Seedling	*Prunus serotina* Ehrn.	PRUSDL
Hemlock Seeding	*Thuja occidentalis* L.	THUSDL
Cedar Seedling	*Tsuga canadensis* (L.) Carr.	TSUSDL

Appendix IX. Average diameter-breast-height (DBH) of trees (≥ 2.5 cm) by site for 1995. All measurements are in cm. Standard deviations are in parentheses.

Site	Average DBH of Conifer Trees	Average DBH of Deciduous Trees	Average DBH Overall
104	4.45	7.6	6.8
	(2.8)	(4.8)	(4.5)
109	8.2	4.9	6.8
	(7.8)	(4.1)	(6.5)
120	4.4	5.0	4.9
	(1.7)	(1.9)	(1.8)
209	4.2	6.1	5.7
	(1.3)	(3.1)	(2.9)
212	8.0	5.4	6.3
	(2.2)	(2.7)	(2.7)
216	6.5	4.1	5.9
	(1.9)	(0.8)	(2.0)
217	5.9	4.7	5.2
	(1.3)	(3.5)	(2.7)
225	13.7	4.7	7.7
	(1.6)	(1.6)	(4.9)
318	4.3	5.5	4.7
	(1.3)	(1.8)	(1.5)
321	5.6	8.2	6.6
	(2.0)	(4.0)	(3.2)
324	4.6	8.0	5.2
	(1.7)	(3.6)	(2.5)
330	10.4	7.9	8.5
	(3.6)	(3.9)	(3.9)
413	12.8	5.7	8.7
	(2.3)	(4.1)	(5.0)
415	12.0	4.6	9.5
	(6.1)	(1.6)	(6.1)
424	6.8	0	6.8
	(2.0)	0	(2.0)
432	6.5	8.7	8.2
	(2.1)	(4.4)	(4.0)
436	0	3.4	3.4
	0	(1.4)	(1.4)
531	10.8	6.1	7.1
	(5.7)	(4.4)	(4.9)
532	13.0	6.6	8.5
	(6.0)	(3.1)	(4.9)

Appendix X. Average diameter-breast-height (DBH) of trees (≥ 2.5 cm) by site for 1996. All measurements are in cm. Standard deviations are in parentheses.

Site	Average DBH of Coniferous Trees	Average DBH of Deciduous Trees	Average DBH Overall
212	6.1	6.7	6.5
	(1.9)	(3.9)	(3.3)
225	12.7	8.5	10.5
	(4.6)	(4.5)	(4.9)
302	6.3	10.5	8.8
	(2.5)	(6.8)	(5.8)
307	4.5	9.6	8.1
	(1.7)	(3.8)	(4.0)
309	5.9	2.7	6.3
	(2.1)	(0.2)	(3.2)
311	6.1	5.3	6.0
	(3.7)	(2.3)	(3.5)
401	12.0	7.0	9.0
	(5.1)	(4.8)	(5.4)
406	14.3	12.7	14.0
	(6.4)	(6.4)	(6.3)
408	14.7	7.4	8.5
	(7.4)	(4.6)	(5.7)
410	11.8	9.9	11.4
	(4.4)	(4.9)	(4.4)
423	4.9	6.3	5.6
	(2.4)	(3.7)	(3.2)

Appendix XI. SEARCH FOR SPINE-TAILED LARVAE IN MOOSE FECES FROM MICHIGAN'S UPPER PENINSULA

Methods

A total of 37 fecal pellet groups from 13 different moose (one to four pellet groups per animal) were examined for spine-tailed larvae. Eight of the moose were tracked by radio signal and fresh fecal pellets collected from snow. Five others were found at random or were traced by mortality signal and frozen pellets collected. All specimens were collected between February and May, 1996 or 1997. Care was taken not to collect moose pellets near deer pellets and fecal pellet groups were bagged individually to avoid contamination. Pellets groups were stored individually, frozen, and examined within 5 months of date of collection.

Pellets were thawed partially 20 - 30 min. Approximately 50 g wet weight pellets were examined (mean 49.5, range 40.9 to 55.3 g). Actual number of pellets taken from individual pellet groups ranged from 8 to 17 pellets (mean 10.5). To avoid possible contamination, moose feces had designated glassware, utensils, and wash basins that were not used previously for processing deer fecal pellets. Feces were processed using a modified Baermann technique (Samuel and Gray 1982, Beane and Hobbs 1983, Welch et al. 1991). Pellet groups were weighed, placed in double-layered cheese-cloth, and allowed to stand 24 hr in 300 ml water in clean, disinfected 15 cm glass funnels. Moose feces were processed 1 month after deer pellet examinations had ended and work areas had been repeatedly washed and disinfected.

To avoid contamination between pellet groups, glass funnels were cleaned with soap and hot water while being scrubbed with a bottle brush, rinsed with 95% ethanol, and rinsed again with hot tap water. Plastic petri dishes were cleaned in the same manner. The bottle brush was washed similarly and allowed to soak in a 15% bleach solution between trials. Funnels were tested for contamination, at random, by setting up Baermann funnels containing plain water and processing them the same as fecal pellet solutions and examining for larvae. No larvae were recovered from cleaned Baermann apparati ($n = 6$).

One hundred ml of fluid and sediment were drained into two 50 ml test tubes and centrifuged at 1500 rpm approximately 10 min. The top 30 ml was discarded and the two samples combined by rinsing one sample into the other with 10 ml fresh water and centrifuged 10 min. The top 30 ml was removed and the remaining 20 ml solution rinsed into 6 cm plastic petri dishes with grids etched into the bottom and examined for spine-tailed larvae using a dissecting microscope at 25X

Results

No spine-tailed larvae were found in 37 pellet groups examined from 13 different moose.

Discussion

Based on presence of *P. tenuis*-like larvae in feces of moose, Clark and Bowyer (1987) and Thomas and Dodds (1988) suggested coevolution of moose and *P. tenuis*. The question remains, is there evidence that larvae of *P. tenuis* are shed in feces of moose. Upshall et al. (1987) reported no first-stage (L1s), spine-tailed larvae in moose feces from New Brunswick, but others have (Kurtz et al. 1966, Karns and Jordan 1969, Clark and Bowyer 1987, and Thomas and Dodds 1988). Kurtz et al. (1966) reported larvae of *P. tenuis* in feces from one of 17 wild moose that were necropsied and had displayed clinical signs of neurologic disease. Karns and Jordan (1969) reported spine-tailed larvae in moose feces on a deer free island, Isle Royale, Michigan, and assumed they were those of *P. tenuis*. However, they found only two larvae out of 230 fecal pellet groups examined. This finding was later attributed to contaminated glassware (Lankester 1987). They also reported spine-tailed larvae in feces from moose of northeastern Minnesota, again only 10 larvae were detected in 361 pellet groups examined. They were examining feces from WTD during the same time period, suggesting contamination of the Minnesota fecal data as well. Clark and Bowyer (1987) found spine-tailed larvae in 9.6% of moose fecal groups (*n* = 594) collected in Maine. Although they recognized that L1s could not be distinguished morphologically from other protostrongylids, because of the high prevalence of *P. tenuis* in deer (50%), they suggested that the larvae were *P. tenuis*. They were also examining feces of WTD during the same time period, so contamination was possible. Thomas and Dodds (1988) examined heads and feces from moose in Nova Scotia and found 6.5% of the heads (*n*=92) had adult worms, and 12.7% of the feces (*n*=318) were infected with spine-tailed larvae. However, positive heads were not matched with positive fecal pellets so the larvae could have been from other nematodes of the family Protostrongylidae. More likely, however, it was another case of contamination because they examined fecal pellets of WTD in the same time period and did not specify exclusive methods.

Potential contamination of Baermann apparati is recognized (Lankester 1987, McCollough and Pollard 1993) and suggestions have been offered to avoid this complication (McCollough and Pollard 1993, Whitlaw and Lankester 1995). McCollough and Pollard (1993) found that 12% of 60 Baermann apparati cleaned with soap and tap water, contained small numbers residual larvae (1 to 3). They suggested using only glass funnels and recommend autoclaving whenever possible. Whitlaw and Lankester (1995) compared numerous cleaning agents that were more convenient for field conditions. They found that scrubbing funnels with soap and hot water followed by a rinse of 95% ethanol removed all larvae. Results from studies that report L1s in moose feces should be viewed with caution if methods to avoid contamination have not been stated by the authors, especially if there is evidence that feces of other ungulates were examined at the same time using the same technique.

Review of literature suggests that only on rare occasions can moose survive infection with *P. tenuis* long enough to deposit larvae in feces. If moose serve as definitive hosts of *P. tenuis*, numbers of adult worms in moose would probably be few, suggesting that: 1) few moose would show clinical signs of infection and, 2) few moose would shed larvae, if so probably few in number and intermittently. Smith et al. (1964) found an average of 2.5 worms per moose collected from Nova Scotia and New Brunswick but all displayed signs of neurologic disease. Smith and Archibald (1967) found an average 1.6 worms per infected moose of Nova Scotia and New Brunswick and 86% showed clinical signs. Gilbert (1974), in Maine, found a mean number of 1.9 adult worms in moose and 80% of those infected showed clinical signs. Upshall et al. (1987) found no worms in the heads of two healthy moose, and two adult worms in a moose that showed signs of neurologic disease.

Apparently very low-dose infections cause signs of disease in moose. Two moose at 5 months of age were given three larvae each (Lankester, unpublished, as cited by Lankester and Samuel 1997). They displayed signs of lameness in the front legs and weakness in the hindquarters. These signs lessened within 3 months and single adult worms were located on the brain and spinal chord upon necropsy. Similarly, two moose of 9.5 months of age were given 10 and 15 larvae and exhibited similar persistent signs. Ninety-five days following initial infection, one and three worms were recovered during necropsy, respectively. Perhaps moose can survive low dose infections, however, evidence does not support the idea that moose commonly survive multiple infections that would allow them to deposit larvae into the environment. Even if the parsite-induced neurologic disease did not cause direct mortality, surely these weakened animals would be subject to malnutrition and higher predation in the wild.

Literature Cited

Beane, R.D. and N. T. Hobbs. 1983. The Baermann technique for estimating Protostrongylus infection in bighorn sheep: effect of laboratory procedures. Journal of Wildlife Diseases 19: 7-9.

Clark, R.A. and R.R. Bowyer. 1987. Occurrence of protostrongylid nematodes in sympatric populations of moose and white-tailed deer in Maine. Alces 22: 313-321.

Gilbert, F.F. 1974. *Parelaphostrongylus tenuis* in Maine: II - Prevalence in moose. Journal of Wildlife Management 38: 42-46.

Karns, P.D. and P.A. Jordan. 1969. *Pneumostrongylus tenuis* in moose on a deer free island. Journal of Wildlife Management 33: 431-433.

Kurtz, H.J., K. Loken, and J.C. Schlotthauer. 1966. Histopathologic studies on cerebrospinal nematodiasis of moose in Minnesota naturally infected with *Pneumostrongylus tenuis* American Journal of Veterinary Research 27: 548-558.

Lankester, M.W. 1987. Pests, parasites and diseases of moose (*Alces alces*) in North America. Swedish Wildlife Research Viltrevy, Supplement 1, Part 2: 461-489.

Lankester, M.W. and W.M. Samuel. 1997. Pests, parasites and diseases. Pages 479-517 *In* C.C. Schwartz and A.W. Frazmann (eds.), Ecology and Management of the North American Moose. A Wildlife Management Institute Book, Smithsonian Institution Press, Washington D.C. 733 pp.

McCollough, M.A. and K.A. Pollard. 1993. *Parelaphostrongylus tenuis* in Maine moose and the possible influence of faulty Baermann procedures. Journal of Wildlife Diseases 29: 156-158.

Samuel, W.M. and J. B. Gray. 1982. Evaluation of the Baermann technique for recovery of lungworm (Nematoda: Protostrongylidae) larvae from wild ruminants. Biennial Symposium Notes Wild Sheep and Goat Council 3: 232-243.

Smith, H.J. and R.M Archibald. 1967. Moose sickness, a neurological disease of moose infected with the common cervine parasite, *Elaphostrongylus tenuis* Canadian Veterinary Journal 8: 173-177.

Smith, H.J., R.M. Archibald, and A.H. Comer. 1964. Elaphostrongylosis in maritime moose and deer. Canadian Veterinary Journal 5: 287-296.

Thomas, J.E. and D.G. Dodds. 1988. Brainworm, *Parelaphostrongylus tenuis*, in moose, *Alces alces*, and white-tailed deer, *Odocoileus virginianus*, of Nova Scotia. The Canadian Field Naturalist 102: 639-642.

Upshall, S.M., M.D.B. Burt, and T.G. Dilworth. 1987. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). Journal of Wildlife Diseases 23: 683-685.

Welch, D.A., M.J. Pybus, W.M. Samuel, C.J. Wilke. 1991. Reliability of fecal examination for detecting infections of meningeal worm in elk. Bulletin of the Wildlife Society 19: 326-330.

Whitlaw, H.A. and M.W. Lankester. 1995. A practical method for cleaning Baermann glassware. Journal of Wildlife Diseases 31: 93-95.